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CAMBIAL ACTIVITY AND WOOD FORMATION IN BEECH (*FAGUS SYLVATICA*) DURING THE 2006 GROWTH SEASON

Katarina Čufar, Peter Prislan
University of Ljubljana, Biotechnical Faculty,
Department of Wood Science and Technology, Ljubljana, Slovenia

Jožica Gričar
Slovenian Forestry Institute, Department of Yield and Silviculture,
Ljubljana, Slovenia

ABSTRACT

Cambial seasonal activity and the dynamics of xylem growth ring formation were studied during the 2006 growth season in mature beech (*Fagus sylvatica*) trees at a forest stand near Ljubljana, Slovenia. Cross-sections of tissues taken from living trees at weekly intervals were studied with light microscope. Cambial cell divisions began between 18 and 24 April, the cambium achieved maximum width (10-13 cell layers) at the end of May, and cell divisions ceased between 25 July and 16 August. Dormant cambium contained 3 to 5 cell layers. Fitting xylem increments to the Gompertz function showed that the period of most intense cell production was from 30 May to 6 June 2006. The average width of fully formed xylem growth rings was 2552 μm, and the time necessary for their formation was 100 days. Although the investigated trees were healthy and of comparable age, the parameters of the Gompertz function showed differences in radial growth patterns among trees.

KEY WORDS: European beech (*Fagus sylvatica*), cambium, wood formation, cell differentiation, xylem growth rings, Gompertz function, light microscopy

INTRODUCTION

Beech (*Fagus sylvatica* L.) is one of the most important tree and wood species in Slovenia. It grows practically everywhere except in the Mediterranean area and on the highest mountains. It is represented in various ratios in 70% of Slovenian forests. In 2001, beech represented 32% of the entire Slovenian wood stock (Brus 2005). Its percentage is currently increasing because of its great competitive strength, particularly on sites in which conifers are declining (Bončina et al. 2003, Brus 2005).

In addition to its importance in forestry and the woodworking industry, beech is interesting for environmental studies. Its frequency, ability to grow on a great variety of sites and its longevity make it an optimal European species for tree-ring studies and for assembling

spatial networks of tree-ring chronologies for environmental topics (Biondi 1992, Rozas 2001, Dittmar et al. 2003, Piovesan et al. 2005, Lebourgeois et al. 2005, Di Filippo et al. 2007).

Annual growth rings in the wood archive the effects of the dominant environmental factors during wood formation. To discover the relationship between climatic factors and individual developmental processes, and to interpret them, it is important to understand the dynamics of cambial activity and the development of cells in the wood (García-González and Eckstein 2003, Frankenstein et al. 2005, Fonti et al. 2007). Recent wood formation investigations on a cellular level in other tree species (mainly conifers) have confirmed the significance of this knowledge for dendroclimatological and dendroecological studies (Antonova and Stasova 1993, Horacek et al. 1999, Schmitt et al. 2000, 2004, Deslauriers 2003, Rossi et al. 2006a, 2007, Gričar 2007, Marion et al. 2007).

Despite beech's frequency and importance, little is known about wood formation on a cellular level in this species. A few recent articles related to this topic have been devoted to beech from northern Germany (Schmitt et al. 2000) and the Netherlands (van der Werf et al. 2007). It has furthermore been shown that vessel dimensions can be used as an ecological variable and can assist understanding of how internal and external factors govern the development of wood (Sass 1993, Sass and Eckstein 1995, Eschrich 1995). Such studies have shown that investigating wood formation and its structure can provide more information than analyses of tree-ring widths only.

Cambial activity and wood formation have not yet to our knowledge been studied in beech from the SE part of Central Europe. Our research was carried out on six adult beech trees at a typical forest site near Ljubljana, Slovenia, and the objective was to present:

- the seasonal dynamics of cambial activity,
- the formation of 2006 xylem growth ring on a cellular level, and
- the dynamics of xylem growth ring formation fitted to the Gompertz function.

MATERIAL AND METHODS

The study was carried out at a forest site, Panška Reka, near Ljubljana (approx. 46°N, 14°40'E, 400 m a.s.l.). The site belongs to *Blechno fagetum* forest association. The predominant tree species is beech (*Fagus sylvatica* L.). Its proportion is currently increasing, due to the progressive decline of Norway spruce (*Picea abies* Karst.).

We selected six isolated, dominant or co-dominant, healthy beech trees with approximate diameters of 40-50 cm, heights of 25-30 m, and ages above 100 years. Intact tissue samples were taken at breast height at weekly intervals from April to September 2006.

The samples (25 x 10 x 10 mm) were taken from living trees with a chisel and knife. They contained phloem, cambium and outer xylem. In order to avoid the effect of wounding the distance between neighbouring samples was at least 10 cm, so that the new sample would not contain traumatic tissue or wound-wood, which can be formed as a response of the cambium to mechanical damage (Gričar 2007). The tissues were fixed in FEA (formalin-ethanol-acetic acid) solution immediately after removal from a tree.

After one week of fixation in FEA, the sample blocks were reduced to dimensions of 2 x 2 x 3 mm. They were embedded in paraffin using a Leica TP 1020-1 tissue processor for dehydration in a graded series of ethanol (70%, 90%, 95% and 100%) and bio-clear (D-limonene) for paraffin infiltration (Rossi et al. 2006b). Cross-sections of 12 μm thickness were prepared on a Leica RM 2245 rotary microtome, using disposable Feather N35H blades.

For better adhesion of the sections, slides were pre-treated with albumin. Sections were dried at 70°C for half an hour and cleaned of residual paraffin by immersing the slides in bio-clear and ethanol. Sections were finally stained for light microscopy with safranine and astra blue dissolved in ethanol and mounted in Euparal.

A Nikon Eclipse 800 light microscope (bright field and polarized light) and a Lucia G 4.8 image analysis system were used for observations and semi-automatic counting and measuring of cells and tissues at various stages of their development.

We followed the seasonal dynamics of xylem formation by distinguishing among cambial cells, differentiating cells (vessels, fibres, axial parenchyma, ray parenchyma) in postcambial growth, secondary cell wall deposition and lignification, and mature cells.

The measurements were done in the cambium and in the developing xylem growth ring of 2006. We selected three radial files in the cambium in order to count the number of cells and to measure the width of the cambium (in μm). We measured the width of the increment in the current growth ring along three radial files.

In each intact tissue sample, we calculated the average width *(Xi)* of the 2006 growth ring based on measurements along 3 radial lines:

$$X_i = \frac{\sum_{j=1}^{n} x_{ij}}{n} \quad .....2 \leq n \leq 3 \qquad (1)$$

Xi – average width of xylem growth ring 2006, *i* – date of sampling; n-number of measurements, j – subsequent measurement on individual sample.

The formation of xylem growth ring 2006 was subsequently analysed with the Gompertz function (Zeide 1993, 2004, Rossi et al. 2003) according to equation 2:

$$y = A\ exp(-exp\ (B - k\ t)) \qquad (2)$$

y – weekly cumulative width, *t* – day of the year, *A* – upper asymptote, representing the maximum ring width, *B* – estimated place on x-axis of the onset of cambial activity, *k* – inflection point on the curve representing the maximum daily rate of growth.

All calculations were made in Microsoft Excel, and the graphs were drawn in SigmaPlot 9 software.

RESULTS

Cambial activity

Cambium consisted of radially flattened cambial cells with thin, non-lignified primary cell walls that stained blue with astra blue stain (Fig. 1 a, b). The morphology of the cells and the number of cell layers in the cambium varied throughout the year. Dormant cambium contained 3 to 5 layers of cells with typically rectangular cell walls (Fig. 1a). When the divisional activity of cambium started in the second week of April 2006, the number of cells in the cambium increased to approx. 10 layers and the walls of cells became thinner (Fig. 1b). The number of cell layers remained at that level until 20 June, after which the number of cells started to decrease. Between 25 July and 16 August, cambial divisions ceased and the cambium was only 3 to 6 cell layers wide. The morphology of the cells at that time was similar as before the reactivation.

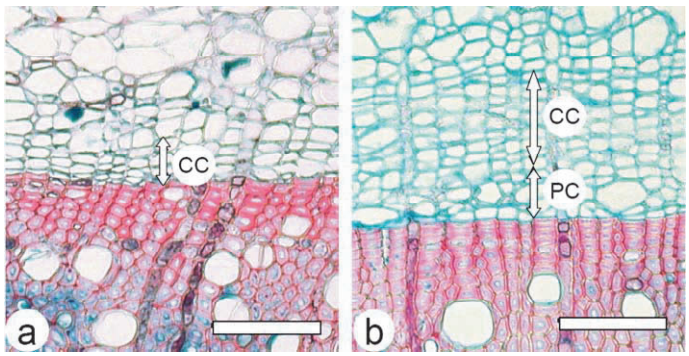

Fig. 1: Cambium (CC) in beech (Fagus sylvatica) in (a) dormant period, consisting of 3 to 4 layers of cells with small radial dimensions and slightly thickened cell walls; below is a part of the fully formed xylem growth ring, above is secondary phloem; (b) active CC with approx. 9 cell layers. The radial dimensions of the cambium cells are slightly enlarged, and the cell walls are thinner than in the dormant period. Below the CC is the current xylem growth ring, the cells are in the phase of postcambial growth (PC). Scale bars = 100μm.

Differentiation of xylem

The xylem in beech consists of vessels, fibres, axial parenchyma and ray parenchyma (Fig. 2a). The vessel elements, fibres and axial parenchyma cells are derivatives of fusiform cambial initials, whereas ray parenchyma cells originate from the ray initials. The cell types have diverse morphology, and reach their final size and shape in the process of differentiation. Newly formed vessel elements and fibres die at the final stage of differentiation, whereas parenchyma cells can remain alive as long as they are a part of the sapwood (Panshin and de Zeeuw 1980).

Cells in the currently formed xylem ring in postcambial growth were defined by larger dimensions and thin, non-lignified, blue stained cell walls (Fig. 2 a-d). Deposition of secondary wall layers was observed in bright field (Fig. 2b) and under polarized light (Fig. 2c). In this phase, the originally thin cell walls started to thicken and the cell walls showed birefringence under polarized light. The beginning of cell wall lignification could be observed as the red stain safranine gradually replaced the blue staining, progressing from the outer parts of the cell wall towards the lumen (Fig. 2 d, e). When the process of differentiation was completed the walls of mature vessels and fibres were completely red stained and their lumina were empty (Fig. 2 d, f).

The first developing vessels in post-cambial growth were observed between 18 and 24 April 2006. Synthesis of the multi-layered secondary cell wall started between 24 April and 3 May 2006. The first fibres in postcambial growth were observed between 18 and 24 April 2006. In the initial phase of differentiation, the fibres had thin primary cell walls and small diameters, and thus resembled the cambial cells. Synthesis of the secondary wall began between 24 April and 3 May 2006, starting in the fibres that surrounded the vessels. Deposition of the cell layers and lignification spread gradually to the remaining tissue. The first fully differentiated fibres were observed between 13 and 20 June, i.e. five weeks after their formation. The development of the latest formed cells continued for some time after the cessation of cambial activity in mid-August. The cell-walls of the fully formed fibres and vessels stained red and their lumina were empty. The development of axial and ray parenchyma was less apparent, because the cells contained cytoplasm and had relatively thin cell-walls during differentiation and when they were fully developed.

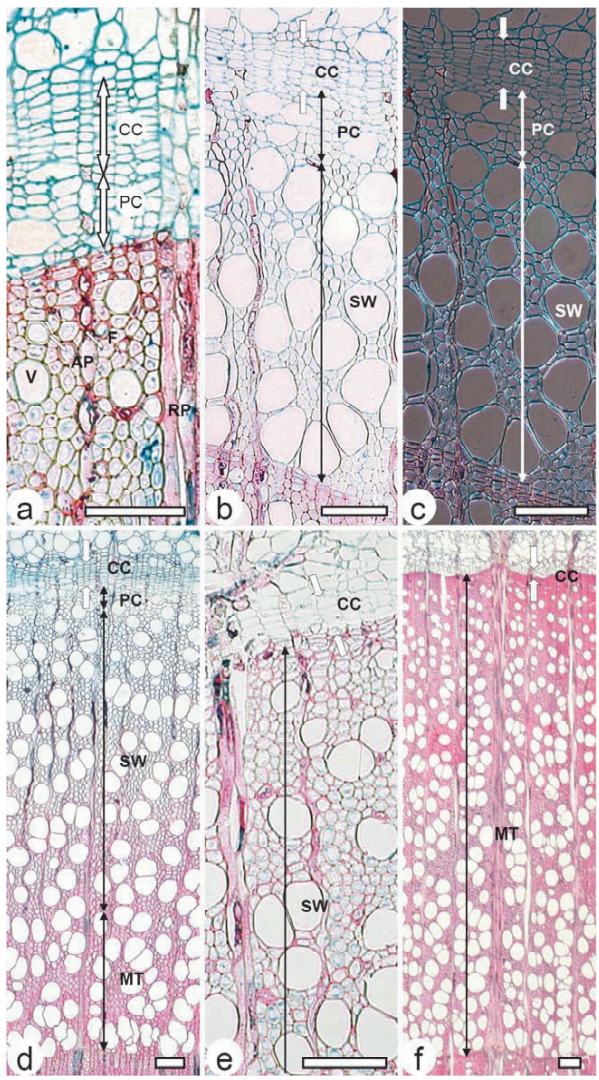

Fig. 2: Phases of xylem ring formation in beech (Fagus sylvatica): (a) cambium (CC) and forming growth ring in wood with cells in postcambial growth (PC) on 24 April 2006; V-vessel, F-fibre, AP-axial parenchyma, RP-ray parenchyma; (b) and (c) wide CC and forming xylem growth ring in the phase of PC and deposition of secondary wall (SW), in the bright field (b) the SW cells are stained red and in polarized light (c) the SW cells show birefringence; (d) CC with reduced number of cells and xylem ring with cells in phases of PC and SW and with completely mature cells (MT). Fully differentiated elements have empty lumina and red stained cell walls; (e) dormant CC and fully formed xylem growth ring on 16 August 2006 with blue stained inner parts of the cell walls of the last formed fibres indicating that the SW phase is not yet completed; (f) narrow CC and fully formed 2006 xylem growth ring. Scale bars = 100 μm

By the week between 20 and 27 June, 75% of the growth ring was completed. According to Sass and Eckstein (1995), the first 75% of the growth ring in beech roughly corresponds to earlywood which gradually transforms into latewood. Between 9 and 16 August 2006, all xylem cells were already formed by the cambium; only the differentiation of the last formed cells (mainly fibres) was not yet completed.

Xylem growth ring formation evaluated with Gompertz function

Data on the growth of the 2006 xylem ring were fitted to the Gompertz function for all six beech trees (Fig. 3). Despite differences among trees, the averaged values of xylem growth fitted 98.7% to the Gompertz function. The calculated final growth ring width was 2552 μm (average of all trees). It varied from 1944 μm (tree no. 2) to 3515 μm (tree no. 1) (Tab. 1).

The rate of increment was 26 μm per day (average of all trees) and varied from 15 μm (tree no. 2) to 35 μm (tree no. 1). Maximum cell production occurred on 29 May (from 21 May to 5 June) (Fig. 3, 4). On average, the beech trees needed 100 days for the development of the majority of the xylem growth ring in 2006. This varied among trees and was from 77 (tree no. 6) to 132 days (tree no. 2) (Tab. 1).

Tab. 1: Parameters of Gompertz function for 2006 xylem ring formation in six beech (Fagus sylvatica) trees near Ljubljana, Slovenia

Parameter	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	Tree 6	Average
Final ring width (μm)	3515	1944	3333	2193	2035	2327	2552
Daily rate of wood formation (μm)	34	15	32	25	23	30	26
Duration of wood formation (days)	103	132	104	87	90	77	100

The time of cessation of wood formation calculated from the Gompertz function slightly deviated from the time determined by observations of cambial cell divisions under the microscope. In all cases, the cambium stopped producing new cells 2 to 3 weeks later than calculated by the Gompertz function. The deviation occurred because the rate of cell divisions markedly slowed towards the end of cambial activity and only few cells were formed over a lengthy period, contributing only slightly to the final width of the xylem growth ring.

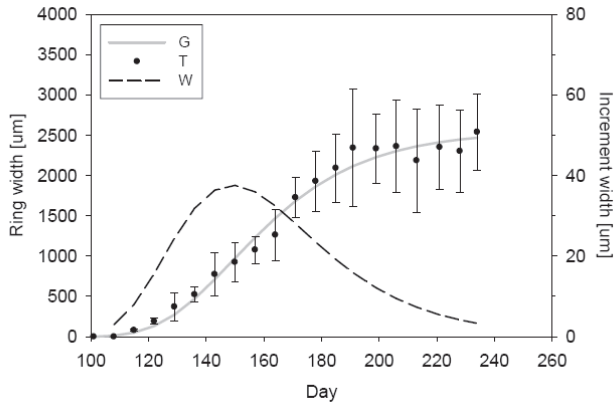

Fig. 3: Dynamics of wood formation in the 2006 growth period averaged for six beech (Fagus sylvatica) trees near Ljubljana, Slovenia. (G) Gompertz function, (T) averaged values with ± 95% confidence intervals, (W) increment, (Day in the) of the year (day 100=10 April, day 240=28 August)

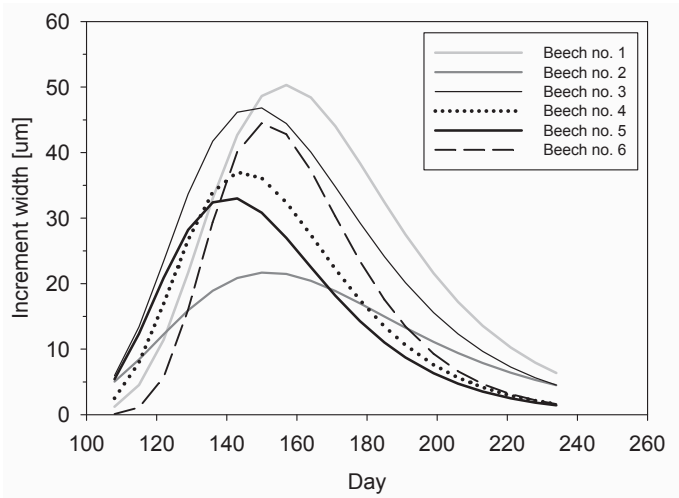

Fig. 4: Increment of wood in 2006 growth period for six beech (Fagus sylvatica) trees near Ljubljana, Slovenia. (Day in the) in the year (day 100=10 April, day 240=28 August)

DISCUSSION

Xylem growth ring formation at breast height of the investigated beech trees started on 18 April 2006. The rate of cell divisions was low in the first weeks after cambial reactivation and maximum cell production occurred between 21 May and 5 June 2006. This is in agreement with Eschrich (1995), who reported highest cambial activity in beech between the end of May and middle of June. However, Rossi et al. (2006a) reported that maximum radial growth of various

conifers (*Abies alba*, *Larix decidua*, *Picea abies*, *Picea mariana*, *Pinus cembra*, *Pinus sylvestris*, *Pinus uncinata*) at the timberline occurred around the summer solstice (21 June), when the photoperiod was the longest. Similar results were also observed by Gričar (2007) in *Picea abies* and *Abies alba* growing on different sites in Slovenia.

Sass (1993) and Sass and Eckstein (1995) suggested that wood formation in beech is governed by internal factors in the first part of the growing season and by external factors in the second part of the growing season. Since beech forms the majority of its rings with an adequate amount of vessels in a short period of time at the beginning of the growing season, this is presumably a successful strategy for establishing an efficient water conducting system. The crown is thus supplied with water and possible negative environmental effects on cell division in the second part of the growing season do not endanger the water supply of a tree.

The activation of the cambium in the studied beech trees in 2006 occurred 22 days (3 weeks) earlier than in the beech from the vicinity of Hamburg investigated in 1996 (Schmitt et al. 2000). All phases of wood formation, including the cessation of ring formation that took place in September, were later at the German site than at the Slovenian site. Otherwise, the dynamics of xylem ring formation (i.e. form of the growth curve) was comparable in the two sites. As in Germany, the onset of cambial activity in beech in the Netherlands (experiment done in 2003) was also about one week later than in Slovenia (van der Werf et al. 2007). In the Netherlands, the beech xylem ring grew rapidly from the middle of May until the beginning of July; it then slowed down due to an extremely hot July and August 2003. Growth increased again from mid-September until mid-October (Werf et al. 2007). Later onset and cessation of cambium activity in beech in Germany and in the Netherlands might be due to the different geographic and climatic conditions than in Slovenia.

The duration of growth ring formation in Slovenian beech lasted 100 days and was completed by the end of August. This, for example, deviates from observations in Norway maple (*Acer platanoides*) in Ljubljana in 2005, where growth ring formation continued for 147 days and was completed in mid-September (Marion et al. 2007). In this case, the different duration of ring formation can be ascribed, among other things, to different tree species, age, micro site, and year to year variation of climatic conditions.

Although the investigated beech trees were all healthy and of comparable age, the parameters of the Gompertz function revealed differences in growth patterns among trees. Tree no. 2, for example, had the narrowest ring but the lowest rate and the longest duration of wood formation. On the other hand, tree no. 6 had the shortest period of wood formation but nevertheless formed a relatively wide xylem growth ring.

Our results and the studies discussed above indicate that relatively sparse information is available on wood formation in beech. Time consuming sampling and laborious sample preparation are among the main reasons for this. Studies on mature trees require frequent (in our case weekly) visits to forest stands and destructive collection of tissue samples from living trees.

Despite being several methods available for studying the seasonal dynamics of wood formation, we still do not have an ideal one (Mäkinen et al. 2008). We decided to use the intact tissue sampling method, which has several advantages compared to the frequently used pinning or micro-core sampling (Gričar et al. 2007, Seo et al. 2007, Rossi et al. 2006 b). In our case, the dimensions of the samples were sufficient to prepare cross-sections of adequate size and quality to observe the cambium and the development of individual cells. The disadvantage of the method is that, despite collecting the smallest samples possible, the sampling injured the trees, so it was only possible to do it throughout a single growing season. Extended sampling would endanger the survival of the trees.

On the other hand, the presented results indicate that studying wood formation on the cellular level could answer (and open) many questions regarding the physiology of mature trees.

CONCLUSIONS

We presented cambial seasonal activity and the dynamics of xylem ring formation during the 2006 growth season in mature beech (*Fagus sylvatica*) trees at a forest stand near Ljubljana, Slovenia.

Cross-sections of tissues taken from living trees at weekly intervals enabled us to observe the cambium and the forming wood on a cellular level.

The number of cell layers and the morphology of cells in the cambium enabled us to define whether it is dormant or active. Dormant cambium contained 3 to 5 and active cambium 10-13 cell layers. Active cambium had cells with smaller radial dimensions and thinner cell walls than those in dormant cambium.

We followed the development of newly formed cells (vessels, fibres, axial parenchyma, ray parenchyma) and determined the phases of their differentiation (postcambial growth, secondary cell wall deposition and lignification, formation of mature cells).

Cambial cell divisions began between 18 and 24 April, the cambium achieved maximum width at the end of May, and cell divisions ceased between 25 July and 16 August 2006.

Calculations with the Gompertz function revealed that the period of most intense cell production was from 30 May to 6 June 2006. The average width of the fully formed xylem growth ring was 2552 μm, and the time necessary for its formation was on average 100 days.

We found slight differences in radial patterns of growth ring formation among the six investigated beech trees.

The dynamics of growth ring formation in beech near Ljubljana was different from that in Norway maple, spruce and silver fir from various sites in Slovenia, and in beech from northern Europe (Germany and the Netherlands).

Destructive sampling and demanding tissue preparation are among the main reasons that comparable studies in beech are very rare.

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Katarina Čufar
University of Ljubljana
Biotechnical Faculty
Department of Wood Science and Technology
Rožna dolina, Cesta VIII/34
SI-1000 Ljubljana
Slovenia
Tel: 386 1 423 11 61
Fax: 386 1 423 50 35
E-mail: katarina.cufar@bf.uni-lj.si

Peter Prislan
University of Ljubljana
Biotechnical Faculty
Department of Wood Science and Technology
Rožna dolina, Cesta VIII/34
SI-1000 Ljubljana
Slovenia

Jožica Gričar
Slovenian Forestry Institute
Večna pot 2
SI-1000 Ljubljana
Slovenia