THE ANALYSIS OF RADIAL GROWTH IN STEM OF NORWAY SPRUCE BY MEANS OF DIFFERENT METHODS AND ASSESSMENT OF EFFECT OF CLIMATIC CONDITIONS IN RELATION TO THE GROWTH

Gabriela Vichrová, Hanuš Vavrčík, Vladimír Gryc Mendel University in Brno, Faculty of Forestry and Wood Technology Department of Wood Science Brno, Czech Republic

Jan Světlík Mendel University in Brno, Faculty of Forestry and Wood Technology Department of Forest Ecology Brno, Czech Republic

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ABSTRACT

The study focused on the description of xylem formation in Norway Spruce at the cellular level during 2009–2010 in the area of the Drahanska (vrchovina) Upland. Samples were regularly extracted from the research sites in two growing seasons and the number of newly formed and differentiating cells was established for 30–31 year-old trees and 105–106 year-old trees. The results were used for the description of the dynamics of the growth of trees of different ages. Further, we evaluated the effect of selected climatic factors on cellular growth, based on the differences of the effect of the sum of active temperatures with respect to the age of trees and the changes in the effect of temperatures during the growing season. The second evaluated climatic factor was soil moisture. In addition, the differences between the time series obtained from dendrometers and those obtained from counting of newly formed cells were analysed.

The evaluation of the changes in the effect of the sum of active temperatures on cell formation during the season revealed that the temperatures in the second half of June and the first half of July are of the highest significance. The examination of the effect of temperatures on cell formation confirmed that temperatures have a higher effect on cell formation with a 14-day delay.

KEYWORDS: Radial growth, Norway spruce, xylogenesis, dendrometers, climatic factors.

INTRODUCTION

Growth of multicellular organisms is seen as an expansion of an individual's volume, dependent on formation of new cells. This leads to an irreversible process of the expansion of the dimensions of a plant body. Secondary growth is referred to as radial growth and is dependent on cambium activity (Larson 1994). Cambium is a secondary meristem which divides phloem cells centrifugally and xylem cells centripetally (Larson 1994, Zimmermann and Brown 1971).

The process of cell growth and the related issues have been dealt with by many authors. Physiological and biomechanical processes of phylogenesis were described e.g. by Little and Savidge 1987, Lachaud 1989, Cattesson 1989, Savidge 1996. Timing of cell growth was explored e.g. by Roberts et al. (1988), Wodzicki (1971), Horáček et al. (1999), Gryc et al. (2011), Vavrčík and Gryc (2011). The aspect of cell growth as an indicator of health condition was discussed by Gričar et al. (2009).

Cambium activity is dependent on a number of internal (e.g. the genetic prerequisites of the plant, its health condition, age and part of plant) and external factors (Panshin and de Zeeuw 1980). Wodzicki (1971) divided the external factors into (1) basic conditions for xylogenesis (temperature, water, nutrients in the soil, gravitation, photoperiod) and (2) random factors (wind, fires, frost, floods, defoliation). Many authors emphasize the effect of climatic conditions on the final diameter of fibres and thickness of the cell wall (Denne and Dodd 1981, Philipson et al. 1971, Horáček et al. 1999).

A forming tree ring does not consist of a unified layer of cells; each cell divided from the cambial zone passes through several growth stages, which can be distinguished by a light microscope as zones in the cross section. The xylem cells differentiated from the cambial zone get into the zone of radial expansion (G), where living cells expand their radial dimensions. In the maturation zone (D) the radial growth finishes, the secondary cell wall begins to be formed and then lignifies. Gradually, programmed death of cells occurs. In the last zone, the zone of mature cells (T), the cells do not change their dimensions and form fully differentiated tissues (Wodzicki 1971). At each of the development stages, climatic factors manifest different degrees of impact. In temperate areas temperature works as a limiting factor at the beginning of the growing season; it affects the reactivation of the cambium and its activity at the beginning of the growing season (Priestley 1930, Bannan 1962, Wareing 1958, Kozlowski 1971, Fritts 1976).

Horáček (1994) concluded lack of water has a significant effect on the final radial dimension of tracheids in spruce. Radial expansion is dependent on the accumulation of vacuoles into one central vacuole, and this process is influenced by an active water intake (Kozlowski 1971, Kozlowski et al. 1991); water brings an increased osmotic pressure on the cell walls and thus cell radial expansion. The final thickness of the cell wall is related to temperature (Larson 1967), which affects the synthesis of substances necessary for the cell wall formation, storing of new polysaccharide chains and thus the cell wall growth (Salisbury and Ross 1991). While temperature and moisture affect chemical and physical rate of growth processes, the indirect effect of temperature on photosynthesis, breathing, sweating and related processes is also highly significant. Therefore, temperature and water manifest positive correlations provided that neither of these factors is limiting (Horáček et al. 1999).

The resulting structure of a tree ring in wood represents a record of the impact of the main environmental factors which affected the cambium activity in the specific growing season (Schweingruber 1990, Rybníček et al. 2010). In order to be able to interpret the record, we need to know the dynamics of the cambial activity and the dynamics of wood cell development (Horáček et al. 1999, Fonti et al. 2007).

This project explored the dynamics of the secondary xylem formation in Norway spruce – *Picea abies* (L.) Karst. Further, we examined to what degree it is affected by selected external and internal influences. We studied xylem formation in stands of various ages from the same site – age was selected as an internal factor. Out of external factors, temperature and soil moisture were chosen and the degree of their impact on cell growth was examined. The last step of the study was to compare two temporal series of wood growth during a season. The first series originated from a gradual counting of cells in a growing tree ring during the season; the second series originated from measuring by band dendrometers.

MATERIAL AND METHODS

The samples for the study were obtained on research sites of the Institute of Forest Ecology of the Mendel University in Brno, about 30 km to the north of Brno (coordinates N49°29'31''; E16°43'30''). The research area is located in the natural forest area 30 Drahanská vrchovina, forest altitudinal zone 5 (fir-beech). The bedrock consists of intrusive rock acid granodiorite of Brno Massive (Hruška 1980), soil type is modal oligotrophic Cambisol (Němeček et al. 2001). The sites are at an altitude of 600–660 m a. s. l. and in a moderate climatic region (Quitt 1971). The average annual temperature of air is 7.6°C and average annual precipitation is 717 mm (Hadaš 2002). Biotic factors of the environment are regularly monitored on the sites and temperature and moisture are measured daily.

The basic material for the study consisted of several types of data. First, it was sampling for xylogenesis evaluation, then data obtained by means of dendrometers, and finally, meteorological data.

Material for xylogenesic evaluation

The material was obtained in 2009–2010. Samples were taken regularly during the entire growing season (March–September). Six Norway spruce (*Picea abies* (L.) Karst.) trees were chosen from a young stand and six trees from an old stand (dendrometric data and the age of stands are presented in Tab. 1). The samples were always taken from the same trees, in weekly intervals. The objective of sampling was to create permanent preparation which could be used for the determination of the number of cells. Sampling was carried out by means of Trephor (Rossi et al. 2006).

The samples were processed based on the methodology by Gričar (2007), with a slight modification. The samples were put in the conservation solution FAA (formaldehyde - acetic acid - ethanol), then rinsed with water and leached in the first alcohol series. Afterwards, they were put in wax. Thus the handling of samples was easier and cutting using the rotation microtome (Leica RM2235) could be more precise. Then the second alcohol series followed connected with dying in safranin and astra blue, mounting in Canada balsam and producing a microscope slide.

In the prepared slide, three radial rows of tracheids were selected and the numbers of cells in the cambial zone (C), zone of radial expansion (G), maturation zone (T) and zone of mature cells (D) were established.

Data from dendrometers

In the research area, 20 trees were selected for measuring of girth increment by mechanical band dendrometers (EMS Brno). The changes in trunk girth at breast height were recorded in weekly intervals. Selection of sample trees was conducted with regard to the frequency of girth

classes, i.e. the more numerous girth classes contain more trees. The girth increment can be taken by vernier with a tenth of millimetre accuracy. Measuring was conducted in the older stand (see Tab. 1) in 2010.

Meteorological data

The meteorological data was obtained in cooperation with the Institute of Forest Ecology. They were regular, hourly measuring records of soil moisture at a depth of 30 cm and air temperature at a height of 2 m during the entire year.

Stand reference	Young stand "m"	Old stand "s"	
Sampling time	2009–2010	2009–2010	
Stand age at the time of sampling (in years)	30-31	105–106	
Mean breast height diameter (cm)	22.5	36.9	
Mean height (m)	17.6	35.6	

Data processing

Comparison of growth dynamics in trees of various ages

In this step the number of formed cells and the rate of their formation during the growing season were evaluated. In order to prevent deviations caused by random error, Gompertz function (Rossi et al. 2003) was applied to the time series originating from the cumulative numbers of cells of individual trees in the form:

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

where: y – weekly cumulative sum of cells,

t - time computed in Julian days,

A – upper asymptote of the maximum number of cells,

ß – x-axis placement parameter,

 κ – rate of change parameter.

The results for both years were evaluated separately; no significant differences were found; therefore, only the data of 2009 are presented. The calculation was conducted in TableCurve.

Further, the variability of cell formation was explored (characterized by the standard deviation in the results). The progress of cell formation was evaluated by means of graphical representation.

Effect of temperature and moisture on cell formation

The effect of temperature and moisture on cell formation was evaluated using the sum of active temperatures necessary for the beginning of new cell formation, the sum of active temperatures at which the highest rate of new cell formation was reached and the sum of active temperatures at which the cell growth ended. The young and old trees were evaluated separately. The sum of active temperatures was counted since the day when the mean daily temperature exceeded 5° C.

Within the process of examining correlations between cell growth and selected climatic factors, first couples with the highest information capacity (with the highest correlation coefficients) were searched for. The following combinations were investigated:

- Cumulative number of cells the current sum of active temperatures
- Cumulative number of cells the sum of active temperatures with a delay
- Growth rate the current mean daily temperature
- Growth rate the mean daily temperature with a delay
- Cumulative number of cells soil moisture at a depth of 30 cm
- Growth rate soil moisture at a depth of 30 cm.

A suitable delay was searched for using a gradual shift of one type of data from the listed couples and a correlation.

Further, the changes of the effect of temperature and soil moisture on cell formation during the season of 2009 were examined. For this purpose, the all-season time series of cell numbers and temperature sums were divided into month sections, within which correlations were ascertained.

Comparison of growth data obtained by various methods

For this task, the data obtained from dendrometers and the resulting numbers of cells were used.

First, regression dependencies between time series created based on dendrometers and the gradual counting of cells was ascertained. As the dendrometer measuring and sampling for cell analysis was carried out on different days, first the numbers of cells for times corresponding to dendrometer measuring were determined. For calculation the Gompertz function was used.

After regression analysis the results were obtained, the difference in the growth trend of these two types of data was described.

The data of 2010 were evaluated.

RESULTS

Comparison of growth dynamics in treed of various age

Tab. 2: Total numbers of cells and standard deviations for	r indivia	lual stands.
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Store J	Young	Old			
Stand	Number of cells				
Max.	59.75	43.75			
Mean	35.99	26.48			
Standard deviation	23.18	16.68			

When evaluating the total number of cells (Tab. 2 and Fig. 1) it becomes obvious that with an increasing age the number of formed cells decreases. A higher number and variance was found in young trees.

Tab. 3 and Fig. 2 show that in the young stand, besides the higher total rate of cell formation, also the variability of new cell formation rate is higher. In the old stand, the growth rate curve is more even. In the first weeks of cell formation there is a higher rate in old trees; at the end of April the cell formation in the young stand becomes faster and the difference increases until the

end of June.



Fig. 1: Progress of cell formation during growing season 2009 in young and old trees, Gompertz function used.

Fig. 2: Growth rate of the young and the old stand during growing season 2009 of young and old trees.

Tab. 3: Rate of cell formation in individual stands.

Store J	Young	Old			
Stand	Growth rate (number of cells/ wee				
Max.	6.76	4.74			
Mean	2.24	2.00			
Standard deviation	2.50	1.88			

Since then, the rate of cell formation in the young stand decreases; on the other hand, it does not considerably change in the old stand. Starting from the beginning of August, the rate is lower in the young trees, whereas the decrease in rate is less intensive in the old trees.

Effect of temperature and moisture on cell formation

Sum of active temperatures for selected physiological aspects of cell formation

Tab. 4 provides the sums of temperatures necessary for the beginning of cell formation. It is 218 and 383°C in young and old trees respectively, which is a difference of 165°C. The difference of the sums of temperatures at which the highest rate of growth was achieved is even higher - 355° C (young – 936° C, old – 1272° C).

In spite of the difference in the sums of temperatures for the beginning of cell formation and for its highest rate in young and old trees, the timing of these two physiological processes was not significantly different (a difference of 4 days). It means that besides the values of temperature sums, there is also an obvious impact of temperature progress during the growing season. The young and the old trees ended the new cell formation at the same time (sum of active temperatures 2540°C).

Further, we can see the negligible significance of the current mean daily temperatures for the cell formation; the difference between the beginning of cell formation and the highest rate of cell formation in young trees is less than a half degree and the difference between the highest rate of cell formation and the end of cell formation is 0.52°C.

		Young stand	l	Old stand			
	Date	Mean daily temperature (°C)	Sum of active temperatures (°C)	Date	Mean daily temperature (°C)	Sum of active temperatures (°C)	
The beginning of cell formation	16. April	13.93	218.18	30. April	14.84	383.96	
The highest rate of cell formation	11. June	14.4	936.74	2. July	19.42	1272.24	
The end of of cell formation	10. September	18.9	2540.51	10. September	18.9	2540.51	

Tab. 4: Current temperatures and sums of temperatures for the beginning of cell formation, the highest rate of cell formation and the end of cell formation.

The correlation between cell formation and selected climatic factors

Characteristics of cell growth and the external environment between which the highest regression coefficients were found:

Cumulative number of cells - the sum of active temperatures with a delay

Cumulative number of cells - soil moisture at a depth of 30 cm

When the sum of temperatures was used, the calculation included a long-term trend of temperatures. The results were not affected by the current temperature fluctuations. This is also supported by the assertion that temperature is a factor which affects cell formation to a substantial degree indirectly (Horáček et al. 1999).

When searching for the correlation between the cumulative number of cells and the sum of active temperatures, we confirmed that cell growth is mainly affected by temperature, in our case the sum of temperatures, with a 14-day delay (Horáček 1994).

The effect of temperature and moisture on cell formation during the growing season

Tab. 5 shows that in the first half of the growing season there are considerable differences in the dependence on the sum of temperatures between young and old trees. In July both groups manifest the highest dependence (in fact these are temperatures from the second half of June and first half of July, as the data were shifted by 14 days). From this month on, the dependence decreases or slightly decreases to the lowest values within the growing season, in both groups of trees.

The evaluation of the dependence between soil moisture at a depth of 30 cm and the number of cells revealed dependence in April only and this dependence was negative. In spring when the moisture is the highest the formation of new cells only starts.

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Tab. 6 presents the numbers of cells at the particular stages of growth (radial expansion, maturation, mature cells) in particular months.

Month	Sum of to	emperatures	– 14 days	Moisture			
	m	s	Mean	m	s	Mean	
4	0.22	0.22	0.22	0.22	0.37	0.30	
5	0.71	0.25	0.48	0.03	0.03	0.03	
6	0.30	0.12	0.21	0.05	0.01	0.03	
7	1.00	0.27	0.63	0.00	0.16	0.08	
8	0.01	0.03	0.02	0,01	0.03	0.02	
9	0.01	0.02	0.01	0.00	0.01	0.01	

Tab. 5: Correlation coefficients for sums of temperature and moisture and the total number of cells in particular months, where m is the young stand, s is the old stand and mean is the average value.

Tab. 6: Numbers of cells in particular stages of growth.

Growth stage	Radial expansion		Maturation		Mature cells		Total	
Month	Young	Old	Young	Old	Young	Old	Young	Old
4	0.82	0.43	0.00	0.00	0.00	0.00	0.82	0.43
5	4.64	3.12	4.40	0.93	0.03	0.00	9.07	4.05
6	6.28	5.54	13.86	6.75	5.65	1.14	25.79	13.44
7	5.81	5.05	15.70	14.54	31.48	11.20	52.99	30.78
8	3.83	4.33	7.89	9.94	51.15	28.07	62.88	42.35
9	1.00	1.44	1.39	4.71	55.92	45.08	58.31	51.23
10	0.08	0.76	0.11	0.29	57.03	48.45	57.22	49.50

Only the cells of the first two stages – radial expansion and maturation – are active. When comparing the resulting correlation coefficients (Tab. 5) and the numbers of cells, it is obvious that most cells in the maturation zone are found in July and this month also sees the highest impact of temperature on the total number of cells, which supports the statement that temperature mainly affects the stage of radial maturation.

Comparison of tree growth described by dendrometers and the cell xylogenesis

Regression dependence between cell formation and trunk growth described by means of dendrometers.

The resulting determination coefficient for regression dependence between the cell growth and dendrometer measuring (Fig. 3) is $r^2 = 0.80$ for curve $y^2=a+bx^{(0.5)}$.

Fig. 4 captures the progress of growth found by dendrometers and the counting of cells during the growing season of 2010. Both methods describe the same physiological growth process; however, there are differences in the growth dynamics. The growth curve obtained by dendrometers is more even without a marked inflex point, whereas the curve obtained by counting cells approaches a typical S shaped curve with a marked inflex point. The difference in the growth dynamics appears to be the highest in the beginning of the growing season. Cell growth in the beginning of the season is gradual and its rate increases as late as in the second



Fig. 3: Regression dependence between cell growth Fig. 4: Number of cells and radial increment and dendrometer measuring during the growing during the growing season of 2010. season of 2010.

half of June. In contrast to the counted number of cells, the growth described by dendrometers starts at an approximately the same time but then increases with a rate similar to the rest of the growing season.

DISCUSSION

Studies dealing with changes in the water content in tissues suggest/state that the greatest hydration occurs at the beginning of the growing season, then decreases and hits the bottom in the period of summer drought (Čermák et al. 2007, Čermák and Nadezhdina 1998). Hinckley and Bruckerhoff (1975) ascertained that water content in tissues is related to a change in the volume of extensive cell walls. This could be an explanation why the curves obtained from dendrometers of the measured trees revealed growth while a full differentiation occurred later. Tissues were already active enough to respond to the amount of water and a more intensive formation of new cells came later. Another possible reason for differences in these two time series is the differing structure of tracheids during the season. In spring, when earlywood is formed, tracheids with considerably larger radial dimension appear when compared to the second half of the growing season, i.e. the time when latewood is formed. The larger radial dimension at the beginning of the growing season partially balances the smaller number of formed cells.

Spruce on the same sites was studied in 1981–1986 by Lehtonen et al. (2007). He was interested in increments and conducted his research using dendrometers. He reached the conclusion that growth started in late April and finished at the end of September. Dendometric measuring of trees of similar girth conducted in 2010 found the same beginning of growth. Comparing the temperatures in the mentioned years, the mean monthly temperature in April in the period 1981–1986 was 3.27–7.02°C, whereas in 2010 it was 8.5°C. In 2010 growth continued until mid-October, i.e. about 14 days longer than in the former research. The mean temperature in 1981–1986 was 6.8–8.4 and in 2010 it was 7.6°C. The biggest difference in mean temperatures was found for the beginning of the growing season, for April. At the end of the growing season the temperatures were not different. It means that the different temperatures at the beginning of the growing season had no effect on the beginning of trunk volume expansion. The same temperatures at the end of the growing season had no effect on the difference in the time when the trunk expansion finished. These data confirm that temperature is a factor with an effect

which is to a substantial degree indirect.

The effect of temperature on annual growth in *Picea abies* L. Karst. was studied by Troms (Bergan 1994). He ascertained that temperatures in June and July are of the highest significance. Our study established the sum of active temperatures in the same months (second half of June, first half of July) as the most significant, only due to the 14-day delay it was related to cells in July. In this month the maturation zone in a forming tree ring houses the highest number of active cells, which confirms that temperatures are of the highest effect at the maturation stage of cells when they affect the substances vital for the formation of the cell wall.

A forming tree ring does not consist of a homogeneous layer of cells and each growth stage of a cell is differently susceptible to changes in temperature (Larson 1994). Although the effect of external factors changes during the growing season, these changes are manifested within the entire tree ring, as has been also proved in many dendrochronological studies (Schweingruber 1990). The base of dendrochronology is the effect of climatic conditions on the total width of tree rings and this method has been tried and verified in the practice. However, the internal differences in a forming tree ring provide more information on the physiology of the growth of Norway spruce.

Horáček et al. (1999) found out that temperature is a limiting factor at the beginning of the growing season. However, it has been ascertained that trees of different ages responded differently to temperature conditions. When groups of trees of different ages were compared, the sums of active temperatures and the times of cell formation beginnings were different. Old trees started forming new cells at a relatively higher sum of active temperatures than young trees; similar phenomenon was found for the highest rate of cell formation. Timing of these two activities was not significantly different, it means not only the sum of active temperatures but also the progress of temperatures in the season are determining.

CONCLUSIONS

The study describes the differences in physiological processes such as the beginning of new cell formation and the highest rate of new cell formation in dependence on the sum of active temperatures in trees of different ages.

The examination into the effect of temperatures on cell formation confirmed that temperatures have a higher effect on cell formation with a 14-day delay. The evaluation of the changes in the effect of the sum of active temperatures on cell formation during the season revealed that the temperatures in the second half of June and the first half of July are of the highest significance. These temperatures affect cell growth in July, when there are the most cells in the maturation zone. This confirms that the effect of temperature rises at the stage of maturation, when it affects the creation of substances vital for the structure of the cell wall. The dependence between soil moisture and the number of cells was not significant in any month with exception of April (negative correlation).

The comparison of the measuring by dendrometers in 2010 and in the past (1981–1986) with temperatures confirms that xylem growth is affected by temperatures indirectly.

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GABRIELA VICHROVÁ, HANUŠ VAVRČÍK, VLADIMÍR GRYC MENDEL UNIVERSITY IN BRNO FACULTY OF FORESTRY AND WOOD TECHNOLOGY DEPARTMENT OF WOOD SCIENCE ZEMĚDĚLSKÁ 3 613 00 BRNO CZECH REPUBLIC PHONE: 420545134045 Corresponding author: xvichrov@node.mendelu.cz

Jan Světlík Mendel University in Brno Faculty of Forestry and Wood Technology Department of Forest Ecology Zemědělská 3 613 00 Brno Czech Republic