MODELLING EFFECTS OF WEATHER CONDITION ON SEASONAL DYNAMICS OF THE STEM CIRCUMFERENCE INCREMENT IN A MIXED STAND OF NORWAY SPRUCE AND EUROPEAN BEECH

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This study was aimed at modelling seasonal variation of stem circumference increments in a mixed stand composed of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.). Moreover, we focused on the quantification of the main climatic factors governing the increments. The measurements were performed at a site established at about 970 m a.s.l. from the locality of Vrchslatina (Central Slovakia). Data was collected from 20 European beech trees and 20 Norway spruce trees, from 2009 to 2012. The increments (measured at 130 cm above ground level) were recorded circa biweekly using manual band dendrometers. Lognormal function was used for the modelling of the seasonal trend of the increments. Hourly-based records of climatic variables such as air temperature, precipitation, and derived vapour pressure deficit were used for the modelling. The effect of climatic parameters on the seasonal variations of the increments was tested by including them directly into the lognormal function. The results suggest that while the sum of precipitation was a better predicting factor for spruce, the mean temperature was the better predictor for beech. In addition, both temperature and vapour pressure deficits also had an effect on the increments of spruce, but these parameters did not contribute to the explanation of the variability of increments for beech. Overall, the variability clarified by the final model was 72% for spruce and 78% for beech. At the same time, climatic parameters as a part of the model helped to explain 10% of the variability for the spruce (precipitations) and 3% of the variability for the beech (temperature). We also found lower variability in the increments of beech compared to spruce. This suggests that for the specific site conditions spruce are more sensitive to environmental conditions than beech.

Keywords: *Fagus sylvatica, Picea abies*, *seasonal circumference increment, weather conditions, growth modelling*

1. Introduction

For a better understanding of the physiological mechanisms influencing tree growth, sub-daily and cellular scale data (King *et al.*, 2013) or at least repeated measurements at a certain time interval within a year are required. Since the radial growth of trees depends highly on site and weather conditions with inherent variability over growing seasons, one must record growth dynamics in short intervals. Using dendrometers helps to meet these conditions by recording the stem radius at defined time intervals during the growing season. Dendrometers were used by a variety of authors to quantify

the seasonal progress of wood formation (e.g. TARDIF *et al.*, 2001; ZWEIFEL *et al.*, 2005; KING *et al.*, 2013). At first, only mechanic dendrometers were available, but recently electronic dendrometers that are able to record the radial growth of trees in very short intervals (hours or minutes) have been released. However, they measure stem circumference changes rather than wood formation, thus it is difficult to distinguish between true wood formation and hydrological swelling and shrinking (MÄKINEN *et al.*, 2003; MÄKINEN *et al.*, 2008). For instance, KURODA & KIYONO (1997) found that dendrometer measurements did not reflect the seasonal dynamics of xylem growth. MÄKINEN *et al.* (2008) found that according to dendrometers stem radius increases in early May, however the other methods (pinning and microcoring) did not indicate wood formation until late May or June.

During one growing season, the timing, duration and rate of radial growth could differ among species under the same climatic conditions (ROSSI *et al.*, 2006; RATHGEBER *et al.*, 2011). The rate of wood growth (CUNY *et al.*, 2012) and timing of growth onset (LUPI *et al.*, 2010) significantly influence the ring width. From all the abiotic factors that contribute to the different rates and the onset of wood growth, temperature increases induce cambial reactivation for both deciduous and coniferous species (BEGUM *et al.*, 2010). The seasonal growth dynamics were also observed in response to biotic factors, such as competition (LINARES *et al.*, 2009), tree size and social status (RATHGEBER *et al.*, 2011) or tree vigour (GRICAR *et al.*, 2009).

Stem diameter growth at breast height has been proven to be sensitive to stress, especially due to carbon allocation patterns under stress (PRETZSCH, 1989; STERBA, 1996). Relationships between climate and wood anatomy or ring development have been studied at intra-annual time scales in various tree species including black locust (*Robinia pseudacacia* L.) (SCHMITT *et al.*, 2000), beech (*Fagus sylvatica* L.) (SASS *et al.*, 1995; SCHMITT *et al.*, 2000) and Norway spruce (*Picea abies* L. Karst.) (HORACEK *et al.*, 1999; MÄKINEN *et al.*, 2003).

This paper aims at the modelling of a seasonal course of stem circumference increments of European beech and Norway spruce in a mixed pole-stage forest stand. Moreover, it aims at quantifying effects of weather conditions to the seasonal course of increments and analyses inter-specific differences in tree reactions to these factors. The hypotheses to be answered in the study are as follows:

- Is there a difference in seasonal growth patterns between Norway spruce and European beech in a mixed-species stand?
- Are there differences in growth sensitivity to weather condition dynamics over a growing season between the species?
- What are the main weather parameters influencing the seasonal radial growth of the species?

2. Material and methods

2.1. Study area

The research was conducted at the locality of Vrchslatina (Central Slovakia), which was established for long-term detailed experiments for various scientific issues. A more detailed description of the experimental site and forest stand can be found in KONÔPKA *et al.* (2013b).

2.2. Circumference increment measurement

We conducted measurements of stem circumference increments (thereinafter increments) in a mixed beech-spruce stand. The proportion of the beech and spruce (based on a number of trees) in the stand was circa 1:1. The stand was approximately 30-years-old, i.e. in a pole growing stage, with a canopy cover of about 80%. Dendrometer bands, which are commonly used to make short-term repeated measurements of tree-stem growth, were placed on 20 beech and 20 spruce trees in the early spring of 2009. Primarily, the dendrometer increment sensors with a manual reading (type DB20, EMS Brno, CZ), a resolution of 0.1 mm and increment range of 50 mm were used. The bands were placed on the stems 130 cm above ground level. The increments of the trees were recorded approximately biweekly during the growing seasons of 2009, 2010, 2011 and 2012. Consequently, for modelling the seasonal dynamics of circumference increments the mean series for both species were calculated. The mean series was calculated to filter out random effects caused by genetic or other factors that were not possible to account for. Biometric characteristics of both species are listed in Table 1.

2.3. Meteorological data

Using a weather station placed directly in the study area, several meteorological parameters such as air temperature, air relative humidity, precipitation, and solar radiation were measured. Since the increments

Table 1. Biometric characteristics of the species used in the study

Species	Number of trees	Circumference [cm]		Height [m]		Crown base [m]	
		Mean	St.Dev.	Mean	St.Dev.	Mean	St.Dev.
Beech	20	45.6	8.4	10.3	0.7	2.6	0.7
Spruce	20	48.1	6.2	10.5	1.3	2.0	0.8
Total	40	46.9	7.5	10.4	1.1	2.3	0.8

were generally measured at two-week intervals, climatic parameters were adjusted for the respective intervals. Air temperature was averaged and precipitation calculated over the measurement intervals. Moreover, vapour pressure deficit (VPD) was calculated (according to MURRAY, 1967) because it takes into account both air temperature and air humidity and it is usually used for studying plant metabolism and transpiration. Where soil is properly saturated by water, the accepted rule is that the higher the VPD the more intensive evapotranspiration. However, extreme drought causes the closure of stomata which then reduces the transpiration (BUNCE, 1996; CHAVES et al., 2003).

An automatic weather station was established in 2009 to continuously monitor the site conditions of the study area. The meteorological station is situated in an open field near the forest stand used for the dendrometer measurements. Air temperature, relative humidity and solar radiation were measured at a 2-meter height using dataloggers with embedded smart sensors (Minikin TH, RT) manufactured by Environmental Measuring Systems (EMS Brno, CZ). Precipitation was measured by an automatic rain-gauge with a dual-chambered tipping bucket design (Model MetOne 370, Oregon, USA) a collection area of 320 cm² and a resolution of 0.2 mm per pulse. A rainfall gauge was placed at a height of 1 m and all precipitation events were recorded by the datalogger MicroLog ER (EMS Brno, CZ). Temperature, humidity and solar radiation were measured every ten minutes and stored every half hour as an average of the measures.

2.4. Modelling seasonal and cumulative circumference increment

To demonstrate the seasonal dynamics of tree growth during the study period 2009 – 2012 the biweekly records of the increments were used. Since the measurements were done at unequal intervals (generally two-week intervals) we calculated the average increments for the respective intervals and the middle date of the intervals was identified for each measurement. The date of the measurements was changed afterwards to the sequential number of the date during the respective calendar year to avoid a problem with unequal intervals and to allow for regression modelling. A lognormal function was selected for modelling because it is considered flexible and supported by both empirical evidence and theory (CANHAM et al., 2004). This function has been used for modelling potential radial growth by many authors (CANHAM & URIARTE 2006; CANHAM et al., 2006; COATES et al., 2009; BOIVIN et al., 2010):

$$PI_i = a \, exp \left(\frac{-1}{2} \left(\frac{ln(x_1 / b)}{c} \right)^2 \right) \qquad [1]$$

Where PI_i denotes the seasonal increment; x_1 is the factor of a day in the sequence of the particular year; a,

b, and c are regression coefficients to be estimated. In this function the parameter a represents the maximum increment to which the model curve approximates, parameter b is the Julian day when the maximum increment occurs, and parameter c denotes the band of the function (CANHAM et al. 2004). In the following step, we included climate parameters into the function exponent as another independent variable. As a climate parameter we tested both precipitation totals and average temperatures:

$$PI_i = a \, exp \left(\frac{-1}{2} \left(\frac{ln(x_1 / b)}{c} \right)^2 + dx_2 \right) \qquad [2]$$

Here x_2 is the climate parameter and d is the regression coefficient to be estimated. The parameter d was added to the exponent to differentiate the course of the seasonal growth dependent on weather conditions. Precipitation totals and average daily temperatures for the measurement periods (two-week intervals) were used as climate independent variables.

The seasonal growth of the species in the respective year was estimated by a logistic function:

$$CI_i = \frac{a}{1 + b e^{-c \cdot day}} \qquad [3]$$

Where CI_i is the cumulative growth on a particular date of the year; a, b, c are estimated regression parameters; and *day* is the sequential day during the year. The curve has asymptotes $CI = 0$ and $CI = a$. The first derivative of the function expresses the diurnal circumference increment (PI_i) dynamics:

$$PI_i = \frac{a \left(b \left(e^{-c \cdot day} c \right) \right)}{\left(1 + b e^{-c \cdot day} \right)^2} \qquad [4]$$

For detailed analysis of the variability of the increment within a growing season (the variability along the general seasonal trend of the increment) we removed the general seasonal trend of the increment using the lognormal function. The increment index was then calculated by dividing the measured values by the estimated ones. The seasonal course of the increment index was calculated over the precipitation, temperature, and vapour pressure deficit parameters for the measurement periods.

All the analyses were performed using R software (R Development Core Team, 2012).

3. Results

3.1. Seasonal variability of circumference increment

Most of the variability in radial growth of both species occurred from May to the middle of August (Figure 1). When visually compared between the species, there is an obvious similarity between both the spruce and beech, except for increment dynamics in 2009 (Figure 1). Fig-
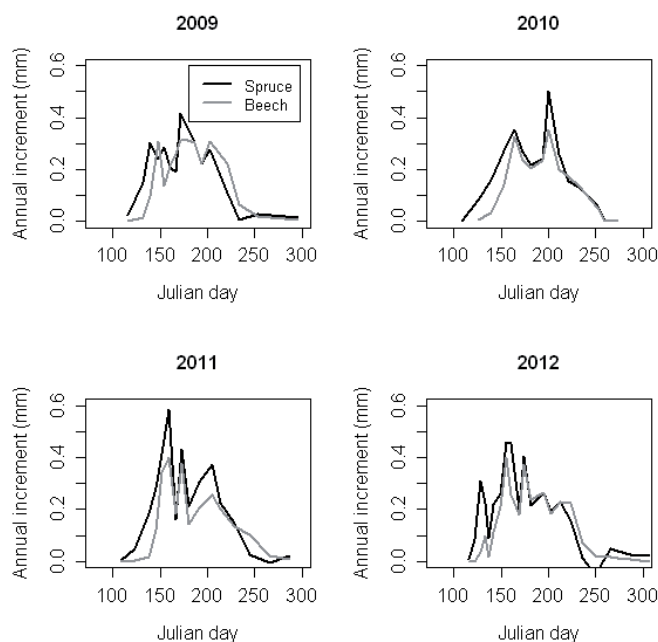
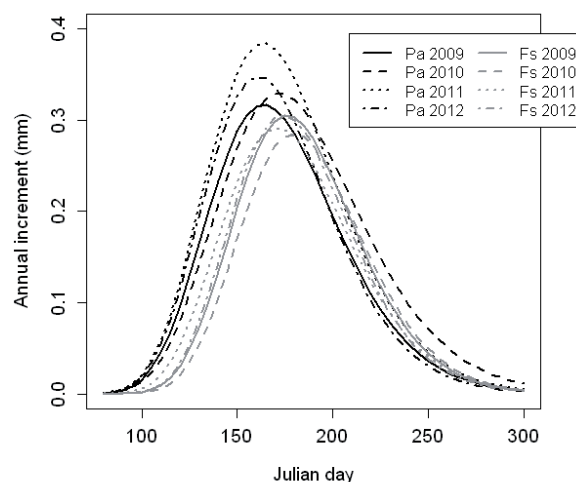**Fig. 1.** Seasonal increment for the species in different years

Fig. 2. Model of seasonal increment of spruce and beech and for different years
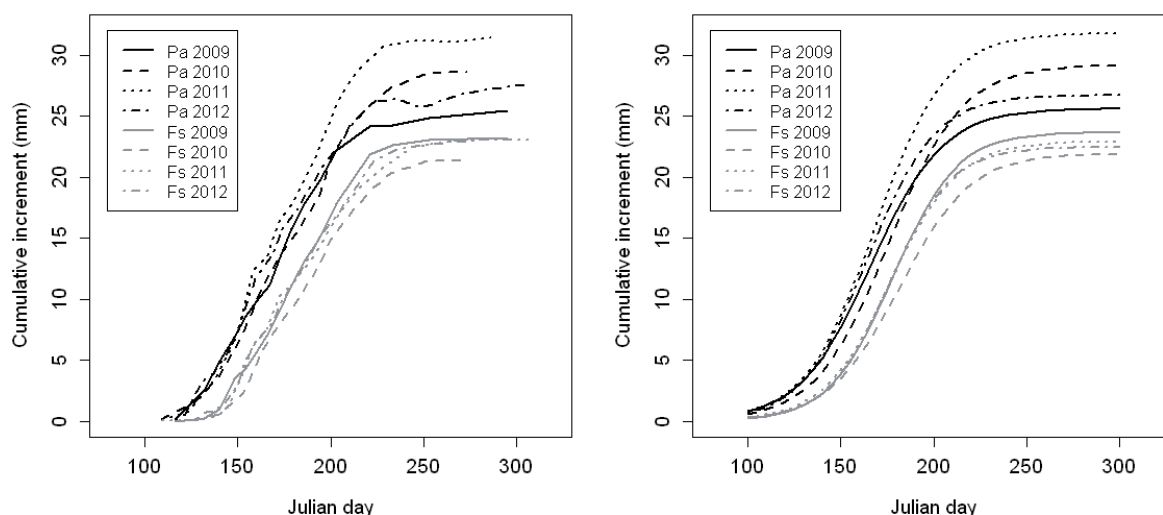

Fig. 3. Cumulative increment for spruce and beech in particular years (left: measured; right: estimated)

ures 2 and 3 show differences in the seasonal dynamics of increments between the species and investigated years. Figure 2 presents the increment, while Figure 3 cumulative growth. Regression parameters as well as "goodness-of-fit" of the models are presented in Table 2. The spruce started to enlarge its circumference earlier in the year than beech, an effect found in all of the study years. The observed inter-annual variability is much higher for spruce than beech, which supports the hypothesis that beech in this site is less sensitive to climate variation than spruce. For spruce the differences of circumference growth between the years with the worst and best climate conditions was found to be over 5 mm, while for beech it

was only up to 2 mm. Moreover, the year with the worst climate conditions was 2009 for spruce, but for beech it was 2010. This finding was unexpected because the climate in 2010 was characteristic for a high amount of precipitation during the growing season, while in 2009 total precipitation was lower compared to the other study years (KONÔPKA *et al.*, 2013b).

3.2. Effect of climate on the seasonal variation of the increment

The base model which expresses only the general increment trend during a year, explained as much as 62% of the variability in spruce (Table 2). The same

Table 2. Estimates and goodness-of-fit of the seasonal increment models including different explaining variables

Species/model	a	b	c	d	R²	DF	RMSE
Spruce							
Base	0.346(0.022)	169.037(2.801)	0.209(0.018)		0.62	65	0.091
Base+temp	0.197(0.064)	161.1(3.264)	0.216(0.018)	0.039(0.022)	0.68	64	0.084
Base+precip.	0.298(0.02)	163.985(2.654)	0.199(0.015)	0.006(0.001)	0.72	64	0.079
Base+VPD	0.409(0.027)	165.375(2.803)	0.221(0.019)	-0.288(0.081)	0.70	64	0.082
Beech							
Base	0.296(0.017)	174.869(2.304)	0.183(0.014)		0.75	64	0.063
Base+temp	0.133(0.044)	171.675(2.507)	0.193(0.014)	0.053(0.021)	0.78	64	0.060
Base+precip.	0.29(0.019)	174.639(2.074)	0.183(0.012)	0.001(0.001)	0.75	64	0.063
Base+VPD	0.325(0.031)	175.196(2.362)	0.19(0.015)	-0.042(0.036)	0.73	54	0.066

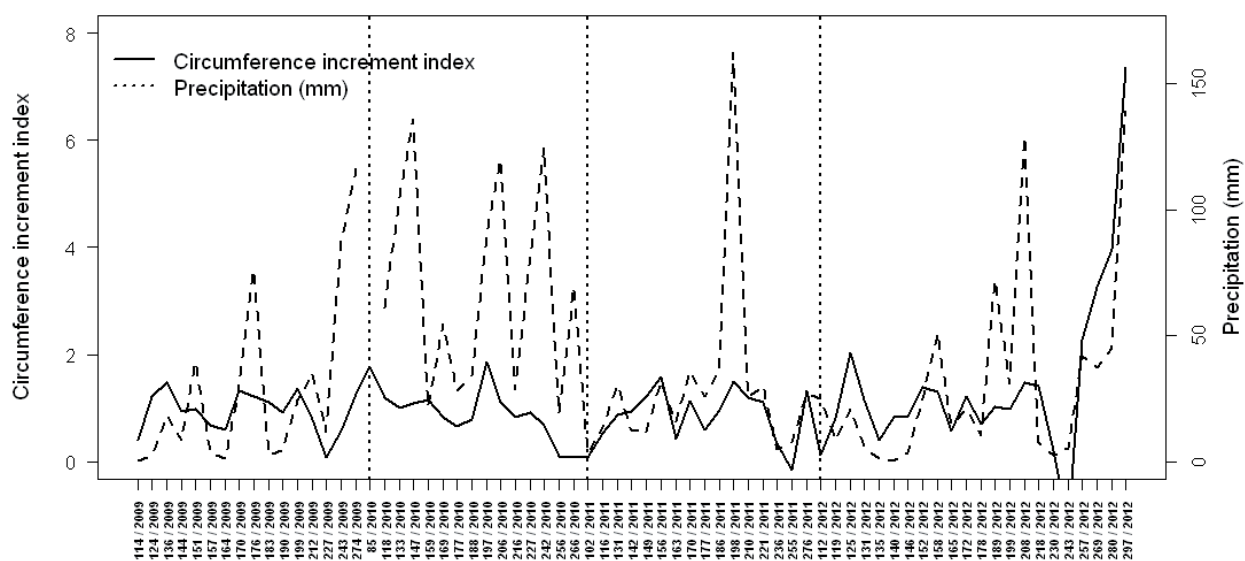*Note: VDP was transformed by natural logarithm.*

Fig. 4. Increment dynamics of spruce and precipitation dynamics during growing season from 2009 till 2012
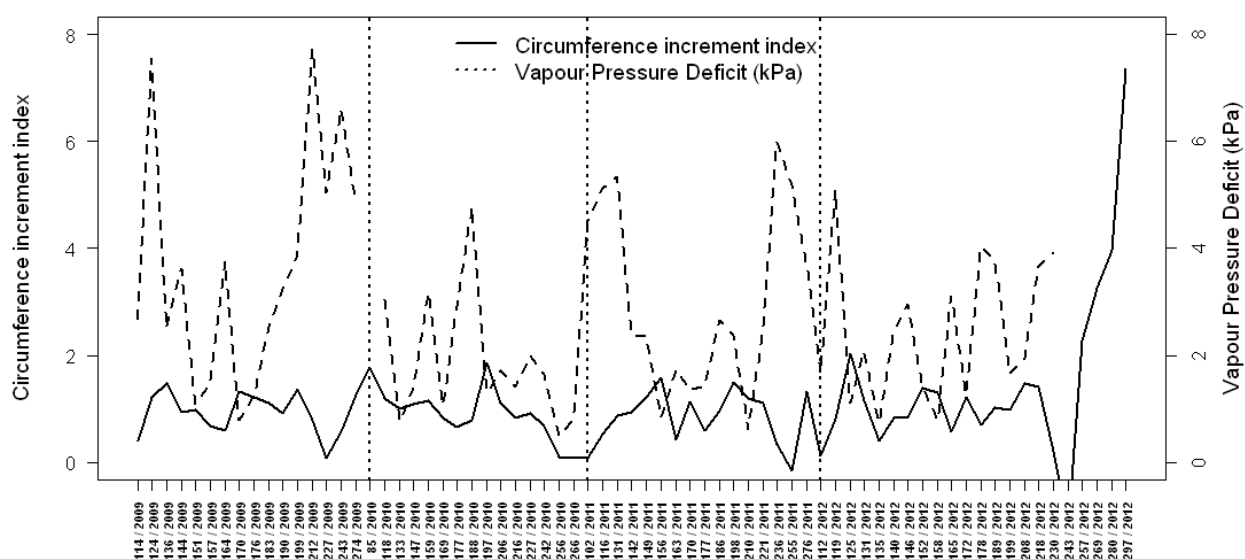

Fig. 5. Increment dynamics of spruce and VPD dynamics during growing season from 2009 till 2012 (VPD as a sum for the respective measurement period)
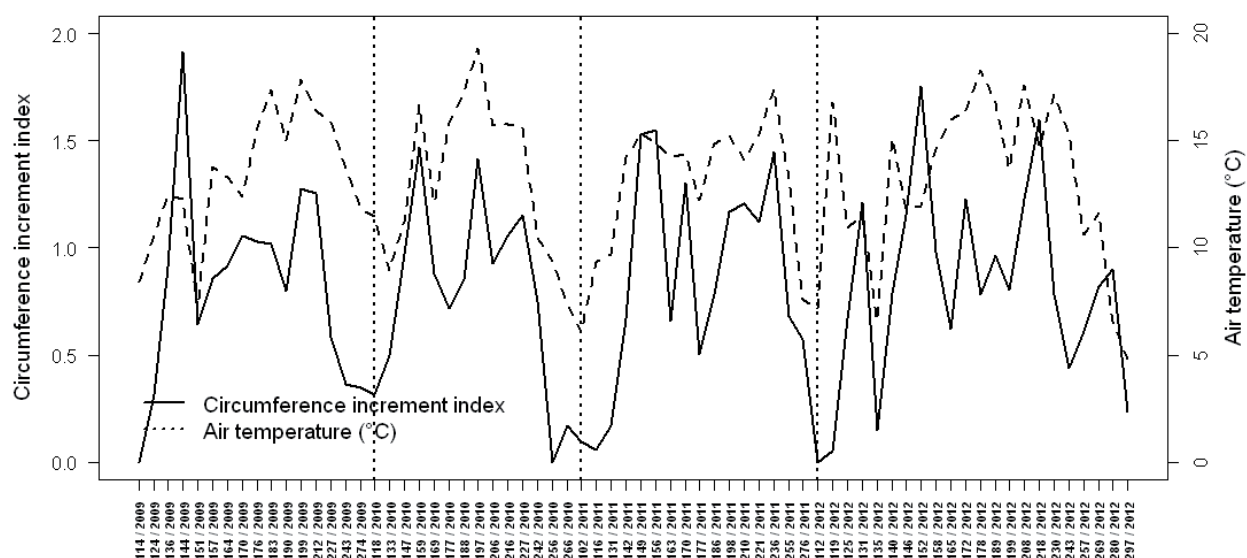
Fig. 6. Increment dynamics of beech and air temperature dynamics during growing season from 2009 till 2012
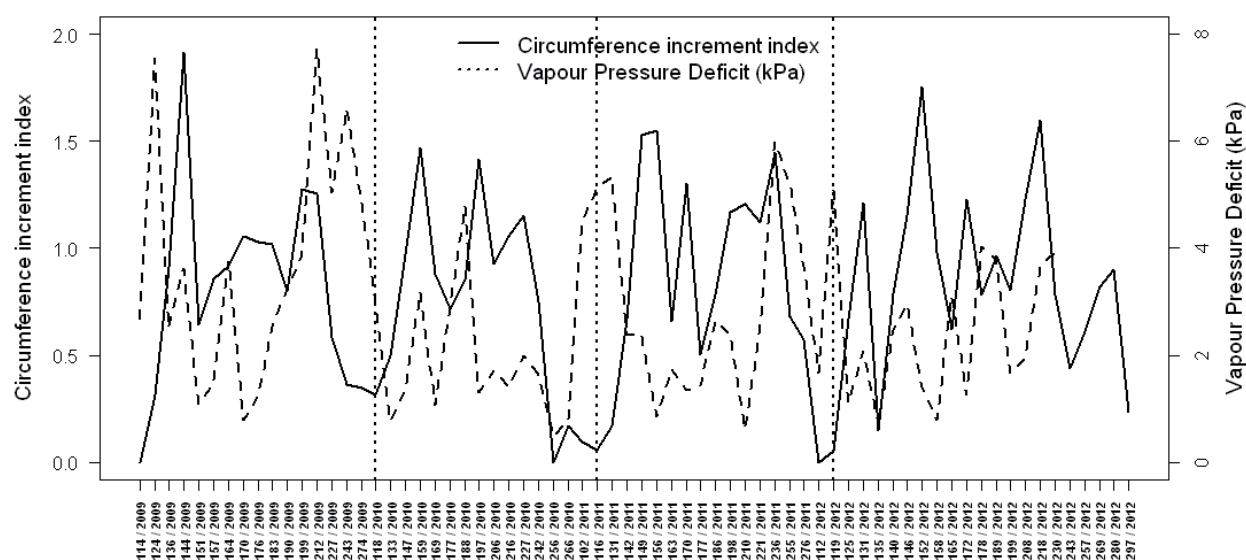

Fig. 7. Increment dynamics of beech and VPD dynamics during growing season from 2009 till 2012 (VPD as a sum for the respective measurement period)

model applied to beech explained as much as 75% of the variability of the increments. While the inclusion of precipitation to the base model for spruce increased the total explained variability from 62% to 72% (resp. 68% when precipitation was replaced by temperature, and 70% when replaced by VPD), the inclusion of precipitation or VPD to the base model for beech did not increase the explained variability at all. For beech, the more important factor affecting the seasonal variability of the increment was temperature (R^2 was 0.78). In addition, the cumulative increment presented in Figure 3 suggested the differences between the species correspond to different climate conditions in different study years.

In spruce, precipitation was found to be a better predictor than temperature and VPD. It is, however, logical since VPD integrates both temperature and air humidity (which is also related to precipitation). In Figure 4, we show a seasonal course of the increment index and precipitation in the respective measurement periods. One can see that the increment increase or decrease follows the increase or decrease in the amount of precipitation quite well. Vapour pressure deficit acted in the opposite way to precipitation (Table 2, Figure 5). For beech, temperature was found to better explain the seasonal variations of the increment (Table 2). From Figure 8 it can be seen that the increment index follows the air

Table 3. Estimates and goodness-of-fit of the seasonal growth models for each year of the study period

Year	Model	R²	DF	MS	RMSE
Spruce					
2009	y = (25.6133)/(1+(5751.07) exp(-(.052065) day))	0.99	13	0.405	0.637
2010	y = (29.1823)/(1+(7868.88) exp(-(.051038) day))	0.99	6	0.113	0.337
2011	y = (31.7857)/(1+(7852.23) exp(-(.053168) day))	0.99	13	0.753	0.868
2012	y = (26.7104)/(1+(10293.7) exp(-(.056129) day))	0.99	14	0.560	0.748
Beech					
2009	y = (23.6742)/(1+(33937.7) exp(-(.058584) day))	0.99	13	0.319	0.564
2010	y = (21.9285)/(1+(14711.5) exp(-(.052849) day))	0.99	6	0.061	0.248
2011	y = (22.9457)/(1+(19327.4) exp(-(.055741) day))	0.99	13	0.703	0.839
2012	y = (22.4709)/(1+(40767.5) exp(-(.060351) day))	0.99	14	0.587	0.766

temperature over the individual measurement periods. Contrary, Figure 9 presents the opposite pattern of increment index and VPD variability.

4. Discussion

In our study we found that the circumference growth of Norway spruce begun earlier than that of European beech. Spruce reached the maximal increment in early June, while beech in later June or the beginning of July. The differences in date when species reached their peak increment between years with different climatic conditions were several days. Čufar et al. (2008) found for European beech in Slovenia that the maximum weekly production of wood occurred between 30 May and 6 June in 2006 and during July, which is not in line with our result. However, Michelot et al. (2012) observed the maximum growth rate of beech occurred in June, which is the month when the leaves reach their maximum leaf mass area and photosynthetic rate, which supported the assumption that beech growth is highly dependent on leaf phenology. We found that air temperature affected the beech circumference seasonal dynamics the most, while Čufar et al. (2008) suggested that precipitation is the driving factor. Urban et al. (2013) suggested that in spring, when soil water is not a limiting factor, tree growth is affected mostly by changes in temperature and the amount of photosynthetically active radiation (also Briffa et al., 1998; Kirdyanov et al., 2003). In late winter and early spring, rising temperatures may increase evapotranspiration, whereby this water loss cannot be replaced by water uptake due to soil frost and it consequently causes a reduced stem radius (Tardif et al., 2001).

The results showed a difference in seasonal growth patterns especially early in the growth season – the spruces set up stem coarsening earlier than the beeches. This tendency is in contradiction to our results on height increments obtained in the young beech and spruce stands located nearby the target mixed stand (Konôpka et al., 2013a). The height increment started much earlier and also finished earlier, in beech approximately four weeks earlier than in spruce. We assume that these differences relate to contrasting growth strategies between broadleaved and coniferous species. While spruce continuously maintains viable foliage (with near immediate access to photosynthesis) after winter dormancy and can invest carbohydrates to stem growth already in very early spring, beech primary invest carbohydrates to building shoots, especially terminal elongation and at the same time to foliage burst.

5. Conclusions

Our results showed a high similarity in the seasonal radial growth pattern between spruce and beech, except for the year 2009. Spruce in this stand started to enlarge their circumference actually earlier than beech in all study years, which is however contradictory to height increments found by Konôpka et al. (2013a). Differences in the annual course of the increments between the years are much higher for spruce than beech, which supports the hypothesis that beech in this site are less sensitive to climate variation than spruce. The most unfavourable climate conditions for the increment dynamics occurred in 2009 for spruce, and in 2010 for beech.

The modelling showed that precipitation explained as much as 10% of the total seasonal variability of the increments of spruce, temperature 6%, and VPD 8%. In the case of beech, only temperature was found to be significant, but explained only 3% of the total seasonal variability of the increment.

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Resumé

Štúdia bola zameraná na modelovanie sezónnej dynamiky prírastku na obvode kmeňov stromov v zmiešanom poraste smreka obyčajného a buka lesného. Okrem toho sme sa zamerali na kvantifikáciu hlavných klimatických faktorov ovplyvňujúcich prírastok. Meranie bolo vykonané na lokalite Vrchslatina (stredné Slovensko) v nadmorskej výške 970 m n. m. Prírastky boli merané na 20 stromoch buka a 20 stromoch smreka od roku 2009 do roku 2012. Prírastok (meraný na 130 cm od úrovne terénu) bol meraný v intervale približne dva týždne pomocou manuálnych denrometrov. Lognormálna funkcia bola použitá pre modelovanie sezónneho prírastku. Záznamy o klimatických premenných, ako je teplota vzduchu, zrážky a deficit nasýtenia vodných pár boli získané z meteorologickej stanice umiest-

nenej priamo na lokalite. Vplyv meteorologických premenných bol testovaný ich zahrnutím priamo do lognormálnej funkcie opisujúcej sezónnu dynamiku prírastku a otestovaním odhadnutých parametrov rovníc. Výsledky ukazujú, že zrážky hrajú dôležitejšiu úlohu pre smrek, avšak teplota pre buk. Taktiež, teplota a VPD majú významný vplyv na prírastok smreka, avšak pri buku rastúcom v daných podmienkach sa ukázali ako nevýznamné. Celkovo, model vysvetlil 72 % variability prírastku smreka a 78 % buka (tab. 2). Meteorologické premenné vysvetlili 10 % variability prírastku smreka, no iba 3 % pri buku.