

Intra-annual patterns of weather and daily radial growth changes of Norway spruce and their relationship in the Western Carpathian mountain region over a period of 2008–2012

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ABSTRACT: The contribution presents the results of a 5-year (2008–2012) dendroecological research in a Norway spruce (*Picea abies* [L.] Karst.) clone forest (Northern Slovakia). Due to different climatic and soil moisture conditions in the monitored years, different seasonal courses of stem increment formation were observed using band dendrometers with continuous data recording. The lack of precipitation affected growth processes mainly during the growth culmination and at the end of summer. The multiple regression analysis of the impact of individual factors on stem circumference changes on the basis of their partial correlation coefficients revealed that the individual environmental characteristics influenced daily stem radial changes with time lags of one to ten days. The results of the analysis of variance showed that the stem radial reactions to climatic and soil moisture factors were not significantly different between the clones.

Keywords: dendrometers; *Picea abies*; environmental fluctuation; Western Beskids; stem circumference changes

Global climate simulation studies predict that, in the future, trees in Europe are likely to experience more severe droughts and higher summer temperatures (IPCC 2001). The trend of climate change over the last 150 years has indicated an increase of air temperature by 0.76°C, and an ongoing decrease of the amount of annual atmospheric precipitation and the annual average relative air humidity (MISTRÍK et al. 2002). One of the most serious impacts should occur in the form of changes in the process of tree growth. Climate affects the timing, rate and dynamics of tree growth. Monitoring how the tree stem radius varies in time can provide insights into intra-annual stem dynamics and improve our understanding of climate impacts on tree physiology and growth processes (DESLAURIERS et al. 2007; SOULÉ 2011; JEŽÍK et al. 2014). The main role in the seasonal diameter changes of trees is played by the vascular cambium. It is known that annual tree rings record the effects of dominant environmental

factors during wood formation (ČUFAR et al. 2008) as they represent the final results of the complete metabolic balance (BECK 2009).

Dendrometers play an important role in the studies of the seasonal activity of vascular cambium, because they are able to measure long time series (SCHMITT et al. 2000; BOURIAUD et al. 2005; JEŽÍK et al. 2014). They are often used to study growth reactions to climatic conditions by recording the stem radius at sub-hourly and micrometer resolution (KING et al. 2013). However, the observed variations represent a combination of growth together with water transport and storage (ZWEIFEL, HÄSLER 2001). The ratio between the amount of water-induced stem radius change and growth-induced stem radius change also determines whether wood growth can be determined by measuring stem radius changes (ZWEIFEL, HÄSLER 2001). The water related fraction represents a short-term effect lasting from a few hours to several weeks, and can have either positive or negative effects on stem

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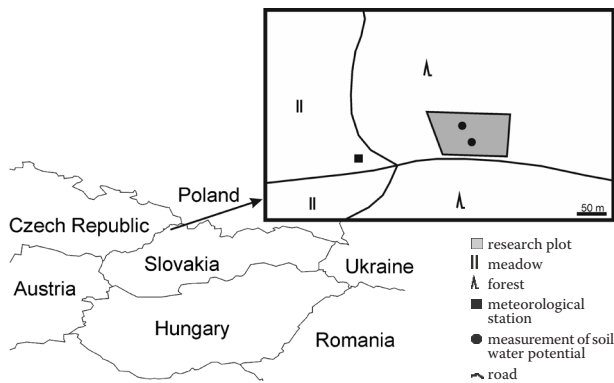


Fig. 1. Location of Predmier I research plot

radius, depending on the changing turgor of stem tissues (ZWEIFEL et al. 2001). The work by DOWNES et al. (2009) provided an excellent overview on measuring stem growth and wood formation. Apart from the external environmental factors, the radial growth is also influenced by a tree growth potential given by genetic properties of trees, their health, age and position in the stand (PANSIN, DE ZEEUW 1980). Tree growth processes with the aim of detecting intraspecies variability were studied e.g. by SONESSON and ERIKSSON (2003), DILLEN et al. (2009), DREW et al. (2009). Spruce is one of the species with high intraspecies and geographical variability (SCHMIDT-VOGT 1978; ERIKSSON 1982; HYLEN 1997). Temperature extremes and changes in precipitation distribution represent the most frequent environmental limits of its production potential, physiological processes and health status (KMEŤ et al. 2008; GE et al. 2013). Since Norway spruce (*Picea abies* L. Karst.) will very likely remain one of the economically most important species in several European countries in the future (MAYER, PRINS 2003), studies of its growth with respect to environmental conditions are very valuable. BOURIAUD and POPA (2009) examined and compared the impact of climate fluctuations on the growth process of three conifer species (Scots pine, Norway spruce and silver fir). They found that air temperature and drought affected Norway spruce to the largest extent.

The contribution of each climatic variable is often influenced, by correlation, with one or more other climatic variables. However, studies that take into account the effects of collinearity are scarce. For instance, DOWNES et al. (1999) studied daily radial stem growth in irrigated *Eucalyptus globulus* and *Eucalyptus nitens* in relation to climate over a 12-month period using multiple linear regression models. In our study we examined the intra-annual pattern of stem radial increase of Norway spruce in the Western Carpathian mountain region and its response to climatic factors and soil moisture with

respect to intraspecies variability. On the basis of the existing information from the literature (ORWIG, ABRAMS 1997; KÖCHER et al. 2012; VIEIRA et al. 2013) we hypothesised that water related factors are the primary factors affecting daily stem radial changes. Our next objective was to detect to what extent the intraspecies variability affects growth strategies of three Norway spruce clones from the aspect of their reaction to environmental conditions at the research site.

MATERIAL AND METHODS

Study area. Our research was performed at Predmier I research plot (49°24'N, 18°35'E, 500 m a.s.l.) situated in the Kysuce – Western Beskids protected landscape area (Fig. 1). Predmier I (0.54 ha) research plot is located on a mild 10% slope of eastern aspect. The forest stand is exclusively composed of Norway spruce. In 2008, the stand was 20 years old. Geological substrate is flysch with varying portions of sandstones, claystones, and marlites. The soil type is Cambisol Podzol about 90 cm deep. From the climatic point of view, this area is situated in the temperate climatic zone with temperate Central-European climate. The area belongs to a mildly warm region with mean air temperature of 6.7°C and mean precipitation totals of 875 mm per year (Fig. 2).

The research plot was established from vegetative reproduction in 1989. The plot was planted with three-year-old cutting transplants taken from the parent stand situated in the Western Beskids. The parent stand belongs to Čadca Forest Enterprise, Predmier Forest District, and is located at 800 m a.s.l. on a southern slope. The planting was performed systematically in a grid of 1.5 × 1.5 m, while 4 transplants from each clone were planted in two repetitions at Predmier I research plot (CHLEPKO 1993 ex STRMEŇ 2004).

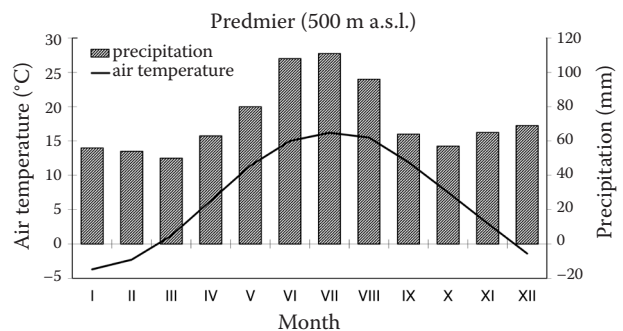


Fig. 2. Climate specification of the region [long-term average monthly data (1961–1990) – air temperature from Čadca weather station (423 m a.s.l.) and precipitation from Turzovka weather station (465 m a.s.l.)]

In the year 2007, 42 trees were selected and marked (6 clones × 7 trees), and their adherence to a specific genotype was tested in laboratory conditions using the polymerase chain reaction (PCR) method. Afterwards, 15 trees (5 trees × 3 clones labelled as clones a, b, and c, hereafter) with similar growth parameters (tree height, and diameter) and of good vitality assessed visually were selected, marked and equipped with dendrometers. The selected tree height was 11.6 m (clone a), 12.3 m (clone b) and 9.8 m (clone c). The average diameter of trees was 12.7 cm (clone a), 11.8 cm (clone b) and 10.4 cm (clone c).

Dendrometers. Data on stem circumferences were recorded using DRL 26 digital dendrometers produced by EMS Brno (Environmental Measuring Systems, Brno, www.emsbrno.cz). The dendrometers were installed on all 15 trees selected at a height of 2.5 m. The measurements were performed from February 2008 to December 2012 with one hour time interval of recording the data into data loggers. The measured stem circumference data were further processed at a daily level. Daily stem radial changes were calculated from the two values measured at 0:00 representing two successive days. Afterwards, the derived daily stem radial changes were summed up in the chronological order to obtain cumulative stem radial changes. Annual values were obtained by summing up daily stem radial changes during one year.

Meteorological and soil characteristics. Weather data [air temperature (°C), global radiation ($W \cdot m^{-2}$) and relative air humidity (%)] were measured at an open space close to Premier I research plot (approximately 200 m from the plot) at 2 m height using Minikin sensors (Environmental Measuring Systems, Brno, www.emsbrno.cz), and were automatically recorded every 10 min. Soil water potential (in bar) was measured at two places within the research plot (Fig. 1) under forest canopy at 15 and 30 cm depths using standard measuring sets consisting of gypsum blocks and MicroLog SP3 data logger (EMS Brno, CZ) with automatic data storage every hour. The measuring set is able to measure SWP in the range from -0.1 to -15 bars. Daily precipitation totals were obtained from two weather stations of the Slovak Hydrometeorological Institute (SHMÚ) – Turzovka (465 m a.s.l.) and Čadca (423 m a.s.l.). From the measured weather data we calculated daily, monthly, and annual values of the parameters. The assessment of weather anomalies (i.e. the comparison of air temperature and precipitation with long-term averages calculated from Čadca and Turzovka weather stations from the period 1961–1990) during the years of the experiment was performed following the methodological regulation of SHMÚ (LAPIN et al. 1988).

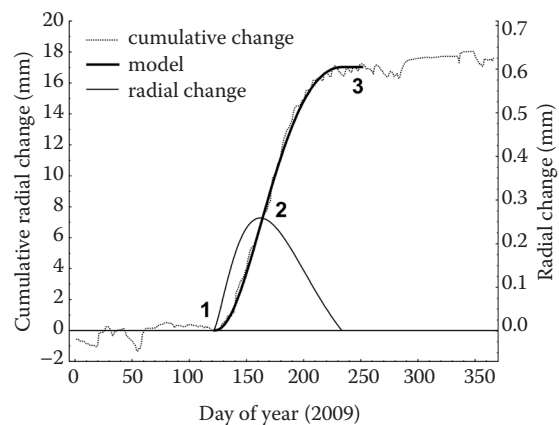


Fig. 3. Characterisation of the main radial growth period for clone b and year 2009

cumulative radial change is derived from the data measured with dendrometers; radial change represents the first derivative of the model fitted to measured data; numbers 1, 2, and 3 indicate the beginning, culmination and end of the radial growth, respectively

The main growth period. The characteristics of the main growth period, i.e. its beginning, end, duration and culmination of the growth, were determined from the cumulative daily stem circumference changes for each clone and each year. This was based on the works of OBERHUBER and GRUBER (2010) and VOLLAND-VOIGT et al. (2011), who considered cumulative increment to be analogous to radial growth.

The beginning of the radial growth is often estimated as a change linked to bud opening and starting transpiration. However, in reality it can be the combination of stem swelling due to rehydration and increment formation, and not the diameter increment (ZWEIFEL et al. 2000, 2006). Due to this, the beginning of the main growth period was identified as the day of the year after which continuous positive development of radial stem changes occurred over a period of minimally 3–5 days, while prior to this day alternating positive and negative fluctuations over a period of 5 days were observed (Fig. 3). Similarly, the end of the main growth period representing the cessation of radial growth was considered the day preceded by continuous positive development of radial stem changes occurring over a period of minimally 5 days and followed by alternating positive and negative fluctuations over a period of 3 to 5 days (Fig. 3). The duration of the main growth period was given as a number of days between the first and the last days of the main growth period. The time series of the cumulative daily stem radial changes (CSRC) during the main growth period, i.e. between the beginning and the end of the growth period, were described using Equation (1):

$$CSRC = a_0 \times (a_1)^t \times t^{a_2} \quad (1)$$

where:

a_0, a_1, a_2 – regression coefficients,

t – number of the day in the main growth period, i.e. t can obtain values from 0 to the length of the main growth period.

The equation explained 99% of the variation of cumulative daily stem circumference changes during the main growth period (R^2 was from 98.9 to 99.7% depending on the clone and the year). The inflection point of the curve, i.e. the point when the curve changes its shape from convex to concave shape, represents the date of growth culmination, i.e. the day when the daily stem circumference change is the highest. The day of growth culmination was considered the day with the maximum value of the first derivative of Eq. (1) (Fig. 3).

Statistical analysis. Statistical analysis was performed on the subset of the data that included the days for which all analysed characteristics were available. The multiple effects of the measured soil moisture and climatic characteristics on diurnal radial changes were examined using multiple regression models. The data used for the multiple regression analysis represented growing seasons only (1 April to 30 October). The analysis was performed for each

spruce clone separately, irrespective of individual years, i.e. all years were analysed together. This approach allowed us to examine the long-term impact of selected environmental characteristics on stem radial changes over a greater range of their values. Multiple regression models included daily soil moisture and climatic factors with a time lag of 1 up to 10 days prior to the analysed stem radial changes. Altogether, we considered 77 characteristics, out of which 6 were basic factors: daily sum of global radiation (*GR*), daily average air temperature (*AT*), average relative air humidity (*RAH*), precipitation (*P*), soil water potential at a depth of 30 cm (*SWP 30*), soil water potential at a depth of 15 cm (*SWP 15*) measured on the same day as the calculated stem radial changes. Further 60 characteristics were derived by shifting the basic factors 1 to 10 days prior to the stem radial changes. In addition, we calculated 11 sums of precipitation totals *SUM-P* for a specified number (two to eleven days) of consecutive days prior to the measured stem radial change. The main presumption of the multiple regression analysis was that each environmental factor could occur in the model only once irrespective of its time lag. It means that all derived regression models contained 7 environmental factors. In total, we calculated approximately 1,600,000 multiple regression models using the Mathcad software, from which we

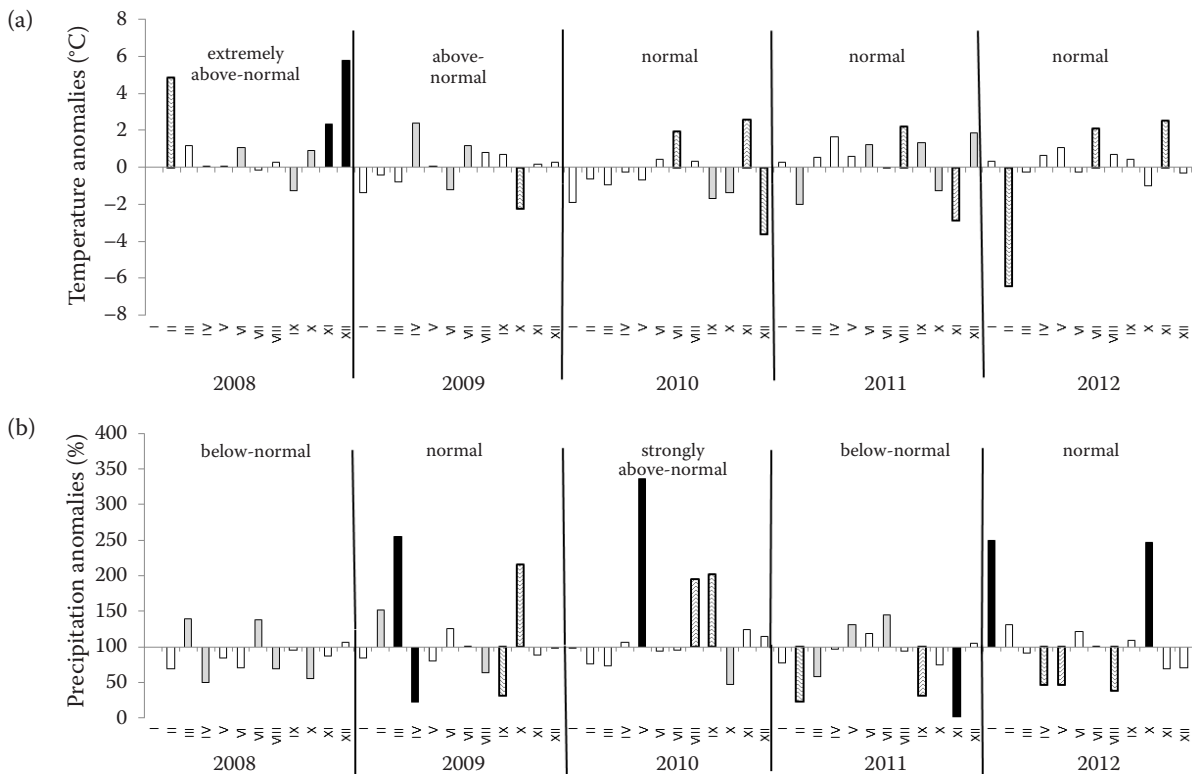


Fig. 4. Normalised monthly temperature anomalies (a), precipitation anomalies (b)

columns: white – within the normal range, grey – non-normal, patterned – strongly non-normal, black – extremely non-normal; text description “normal, below-normal etc.” describes the whole year normality

Table 1. Growth and climatic characteristics in the years 2008–2012

Characteristics	Clone	2008	2009	2010	2011	2012	Mean
<i>SCCH</i> (mm)	a	12.32	20.62	12.13	16.30	13.00	14.87
	b	12.03	17.93	10.41	13.29	14.81	13.69
	c	11.45	15.55	10.04	17.09	15.26	13.88
	mean	11.93	18.03	10.86	15.56	14.36	14.15
<i>LGP</i> (days)	a	119	108	105	122	73	105
	b	103	94	121	120	94	106
	c	116	131	107	103	107	113
	mean	113	111	111	115	91	108
<i>DC</i> (day)	a	163	165	147	163	163	160
	b	157	159	142	160	161	156
	c	159	162	146	137	157	152
	mean	160	162	145	153	160	156
<i>AT</i> (°C)		9.0	7.4	6.2	7.0	6.7	7.3
<i>P</i> (mm)		722.9*	912.2	1179.3	765.8	904.7	897.0

SCCH – cumulative annual stem radial change; *LGP* – length of the main growth period; *DC* – day of the radial growth culmination; *AT* – average annual air temperature; *P* – annual precipitation total; *data available from February to December 2008

selected the best model for each clone. The selection of the model was performed with regard to (1) the overall goodness of fit of the model assessed by R^2 , adjusted R^2 and predicted R^2 , (2) the calculated regression coefficients that represent the partial contribution of the particular environmental characteristic to the explanation of the variance in stem radial changes, and (3) the variance inflation factor (*VIF*) that quantifies multicollinearity between the environmental factors included in the model. Subsequently, the clones were compared with regard to the factors included in the models. Inter-annual and intraspecies variability of tree growth was tested by MANOVA performed in Statistica 7 (StatSoft, Tulsa, USA).

RESULTS

Intra-annual weather and radial growth pattern

In the year 2008, the precipitation was below normal, while the temperature was extremely above normal (Table 1, Fig. 4). The above-normal air temperature and below-normal precipitation at the end of May caused a slight stagnation of radial growth (Fig. 5). The lowest value of soil water potential (-1.13 MPa at a depth of 30 cm) in 2008 was recorded at the end of September (Fig. 5).

In 2009, the whole growing season was normal from the aspect of precipitation totals, although in April and September we observed below-average precipitation totals (Fig. 4) and a reduction of the soil water potential below the wilting point (Fig. 5).

The below-average precipitation at the end of August and in September caused stem shrinking, while above-normal precipitation in October caused stem swelling (Fig. 5).

The year 2010 was contrasting to the previous year 2009 from the aspect of climatic conditions (Fig. 4). In May 2010, we recorded extremely above-normal precipitation totals, while in June and July we observed several rainless periods (Fig. 4). Due to this, growth culmination occurred approximately by 15 days earlier than in the other years (DOY 145, Table 1). Nevertheless, the length of the main growth period was comparable to the other years (Table 1).

The year 2011 was climatically similar to the year 2009. Although the annual precipitation total of the year 2011 was below normal, rainless periods occurred mainly in February and at the end of the growing season (Figs 4 and 5). The main growth period was the longest of all the examined years (Table 1). The amount of soil water available to plants decreased below the wilting point at the end of September and in October (Fig. 5), when the radial growth is usually already finished at the studied site. Therefore, these worsened soil conditions did not negatively affect the stem radial growth (Table 1).

In 2012, both the annual precipitation and the annual average temperature were normal (Table 1). However, the distribution of precipitation during the year was very uneven. While the precipitation in January and February 2012 was above normal, the precipitation during the growing season was below normal. In addition, the temperature in the growing season was above normal (Fig. 4). Due to the lack of rain, the

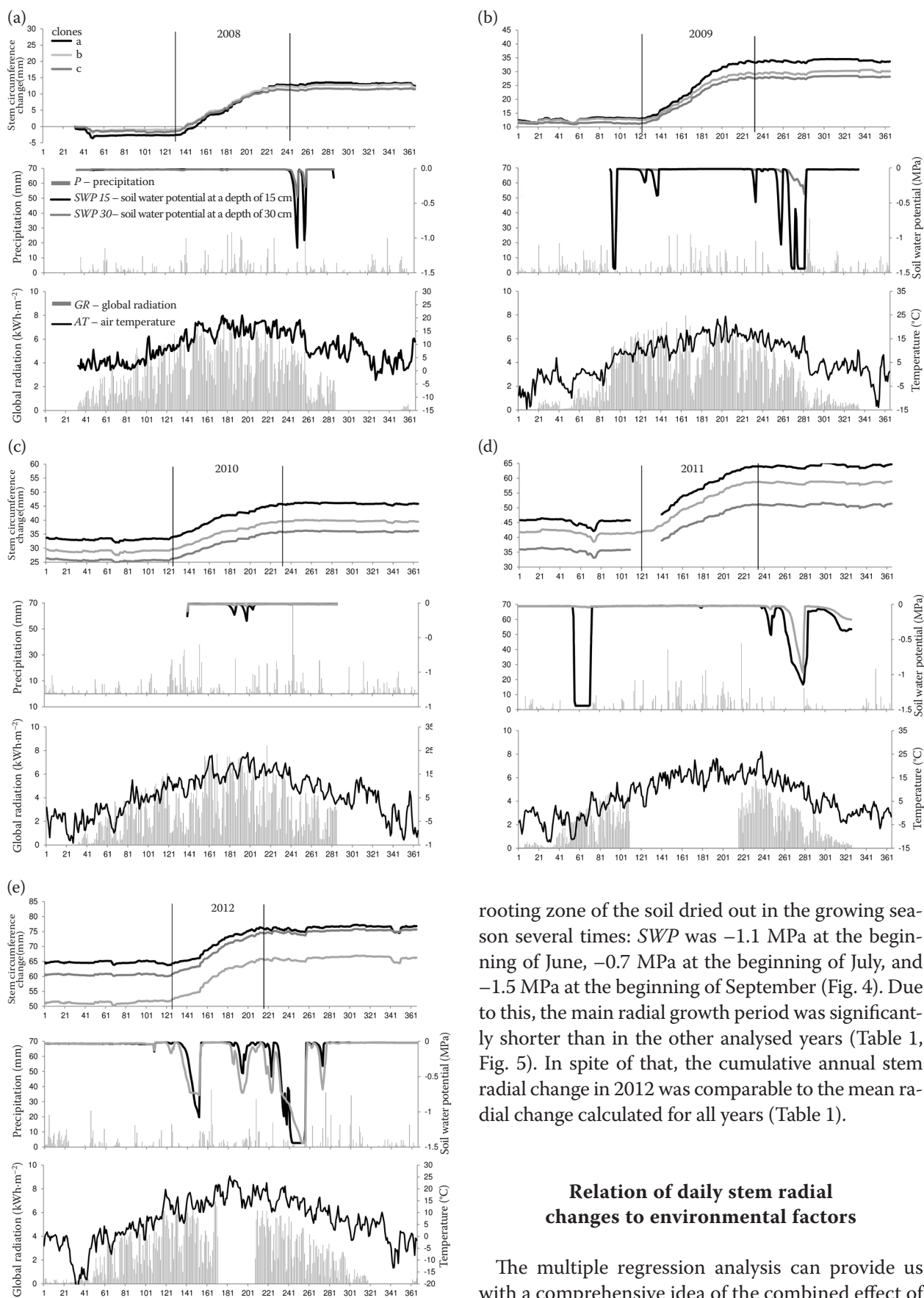


Fig. 5. Cumulative daily stem radial change of *Picea abies* clones and annual pattern of climatic characteristics in 2008–2012; vertical lines – main growth periods during the years

rooting zone of the soil dried out in the growing season several times: *SWP* was -1.1 MPa at the beginning of June, -0.7 MPa at the beginning of July, and -1.5 MPa at the beginning of September (Fig. 4). Due to this, the main radial growth period was significantly shorter than in the other analysed years (Table 1, Fig. 5). In spite of that, the cumulative annual stem radial change in 2012 was comparable to the mean radial change calculated for all years (Table 1).

Relation of daily stem radial changes to environmental factors

The multiple regression analysis can provide us with a comprehensive idea of the combined effect of environmental factors on daily stem radial changes. The results of the multiple linear regression analysis revealed that the highest R^2 reached for clones

a–c were equal to 0.375, 0.332, and 0.328, respectively. The derived models did not show strong multicollinearity between the independent factors, as the maximum variance inflation factor (*VIF*) in the best models was 2.15, 2.34, and 2.10 for clones a, b, and c, respectively. The factors that were included in the best linear regression models were the same for all clones except for one variable in the model for clone b (Table 2): the sum of global radiation one day prior to the stem radial change, average air temperature two days prior to the stem radial change, average relative air humidity three days prior to the stem radial change, precipitation one day prior to the stem radial change, soil water potential at a depth of 30 cm 10 days prior to the stem radial change (*SWP_30cm_10days*), soil water potential at a depth

of 15 cm on the same day as the stem radial change, and the sum of precipitation of the actual day and two days prior to the stem radial change.

The only exception was *SWP_30cm_10days*, which was replaced in the model for clone b by soil water potential at a depth of 30 cm 1 day prior to the stem radial change. The model with *SWP_30cm_10days* was ranked the third for clone b with $R^2 = 0.329$. On the basis of the multiple regression results presented in Table 2, stem radial changes result from stem reactions to the actual soil water potential at a depth of 15 cm, and climatic characteristics of the preceding 1 to 3 days. The analysis of the impact of individual factors included in the model on stem circumference changes on the basis of their standardised (beta) regression coefficients and their partial correlation coefficients revealed that the average air temperature two days prior to the stem radial change had the greatest influence on daily stem radial changes. The second most important factor was the sum of global radiation with one-day time lag, followed by soil water potential at a depth of 15 cm on the same day as the stem radial change, and average relative air humidity with the time lag of three days. Soil water potential at a depth of 30 cm with a time lag of 10 days, and the sum of precipitation of the actual day and two days prior to the stem radial change had the lowest impact on stem radial changes. The partial correlation between the radial changes and air temperature, precipitation and soil water potential at depth of 30 cm was positive (Table 2).

Significant differences in stem radial changes were found mainly between the years 2009 and 2010, and in the case of clone a, the significant differences were also revealed between 2008 and 2009. We presume that these differences were affected by higher precipitation totals in 2010 in comparison with other years (Fig. 4) that were normal or below-normal as for precipitation.

Table 2. The results of the multiple regression analysis indicating the standardised impact of environmental parameters on daily stem radial changes in multiple linear models that explained most variability of daily stem radial changes

Clone	<i>N</i>	Environmental parameter	Statistical characteristics		
			<i>b</i> *	<i>T</i>	<i>P</i>
a	3,710	<i>SWP_15</i>	-0.20	-14.67	<<0.01
		GR with 1 day lag	-0.31	-19.51	<<0.01
		<i>P</i> with 1 day lag	0.23	12.32	<<0.01
		<i>AT</i> with 2 days lag	0.31	20.14	<<0.01
		<i>RAH</i> with 3 days lag	-0.20	-14.02	<<0.01
		<i>SWP_30</i> with 10 days lag	0.04	2.71	<0.01
		<i>SUM_P</i> with 3 days lag	0.11	5.94	<<0.01
b	2,756	<i>SWP_15</i>	-0.22	-12.84	<<0.01
		GR with 1 day lag	-0.27	-13.86	<<0.01
		<i>P</i> with 1 day lag	0.22	9.81	<<0.01
		<i>AT</i> with 2 days lag	0.27	14.30	<<0.01
		<i>RAH</i> with 3 days lag	-0.24	-13.85	<<0.01
		<i>SWP_30</i> with 10 days lag	0.04	2.62	<0.01
		<i>SUM_P</i> with 3 days lag	0.09	4.06	<<0.01
c	3,477	<i>SWP_15</i>	-0.21	-13.92	<<0.01
		GR with 1 day lag	-0.26	-15.06	<<0.01
		<i>P</i> with 1 day lag	0.23	11.45	<<0.01
		<i>AT</i> with 2 days lag	0.26	15.66	<<0.01
		<i>RAH</i> with 3 days lag	-0.19	-12.80	<<0.01
		<i>SWP_30</i> with 10 days lag	0.05	3.08	<<0.01
		<i>SUM_P</i> with 3 days lag	0.11	5.69	<<0.01

N – number of analysed daily stem radial changes, *SWP_15* – soil water potential at a depth of 15 cm, *GR* – daily sum of global radiation, *P* – precipitation, *AT* – daily average air temperature, *RAH* – average relative air humidity, *SWP_30* – soil water potential at a depth of 30 cm, *SUM_P* – sums of precipitation, *b** – standardised regression coefficient, in bold – degree of influence of environmental parameter, *T* – value of *t* criterion, *P* – probability level of significance

Variation of daily stem radial changes over seasons and between clones

The comparison of the annual and daily mean stem radial change of the monitored clones revealed different growth strategies in the individual years (Table 1, Fig. 6). The analysis of variance revealed differences between the individual years (Fig. 6). Significant differences between the individual years were found in clone a (Fig. 6). The highest annual radial increments and daily stem radial changes were found in 2009, while the lowest values were observed in 2010 (Table 1, Fig. 6).

In the first three monitored years (2008, 2009, and 2010) clone a had the highest average annual radial

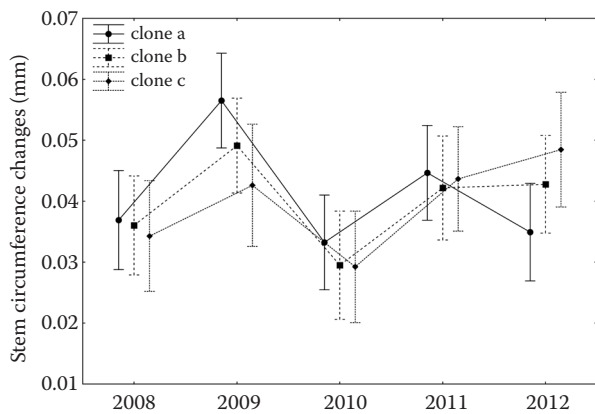


Fig. 6. Average daily stem radial changes of the analysed spruce clones (a–c) in the individual years 2008–2012

increment (Table 1) as well as the highest daily stem radial change (Fig. 6). In the last two years 2011 and 2012, the highest average annual radial increment was found for clone c (Table 1). However, the results of MANOVA analysis indicate that the daily mean radial change reactions of the individual clones to examined environmental factors did not significantly differ in the assessed years (Fig. 6).

DISCUSSION

The observed inter-annual development of radial stem growth presented in Fig. 5 is typical of the trees growing in the temperate region, where the growth occurs during the growing season (MÄKINEN et al. 2003; KING et al. 2013). As reported by MÄKINEN et al. (2003), the seasonal pattern of the stem growth of *Picea abies* (L.) Karst. showed an “S” type curve during the entire growth season, namely, a change in the stem growth rate followed the order of lowly-quickly-lowly. The beginning of the main growth period was observed at the beginning of May (DOY 123–127), which was about one month later than in France, where BOURIAUD et al. (2005) observed that the radial growth of spruce started in early April. In Finland, the first increments in stem radius were reported in April (MÄKINEN et al. 2003; SEVANTO et al. 2006) and May (MÄKINEN et al. 2003).

The culmination of the radial stem growth was observed in June (DOY 153–162) in four out of the five examined years. The maximum radial growth rate in June derived from dendrometer measurements was observed for Norway spruce and other species also by other authors (MÄKINEN et al. 2003; JEŽÍK et al. 2007; KÖCHER et al. 2012). However, MÄKINEN et al. (2003) revealed that the fastest increment in stem radius did not coincide with

the tracheid formation, but with a rainy period. Thus, we assume that the earlier culmination of radial stem increment at our site by 11 days than the 5-year average was caused by the intensive rainy period in spring 2010 (the precipitation total in May 2010 was 337 mm). KNOTT (2004) observed the greatest increment on fir in May.

Growth cessation occurred in August or September with between-year differences of more than 1 month (DOY 204–251). Similarly, BOURIAUD et al. (2005) revealed that the radial growth of Norway spruce trees in France finished in August or September. In Finland, SEVANTO et al. (2006) observed that the last day of the continual tree increment occurred on DOY 289 (October 16). At our site, the radial growth of Norway spruce can last until the beginning of September under favourable moisture conditions, i.e. if precipitation is sufficient at the end of summer, as it was in 2008 and 2010 (Fig. 5). However, if the conditions during the growing season are unfavourable, such as in the dry year 2012, stem radial growth can finish already at the beginning of August (Fig. 5). The results indicate that the lack of precipitation and available soil water affects physiological and growth processes mainly during the growth culmination and at the end of summer, because at the beginning of the growing season trees can utilise water that was accumulated in soil during winter.

The duration of the main growth period substantially varied from year to year (91 to 115 days) (Table 1). Similar investigations were presented by VITAS (2011), who found that the growth of spruce lasts on average 111.8 ± 1.6 days. The shortest main growth period was revealed in 2012 due to the lack of rain during the growing season and subsequent drying of the rooting zone of the soil indicated by low values of *SWP*: -1.1 MPa at the beginning of June, -0.7 MPa at the beginning of July, and -1.5 MPa at the beginning of September 2012 (Fig. 5). In Central European conditions tree growth begins to be limited when *SWP* decreases below values around -0.1 and -0.2 MPa, although the conventionally determined wilting point is set to -1.5 MPa (LARCHER 2003). KNOTT (2004) reported that 70–90% of the annual radial increment was formed until the end of July, while the increment in August and September was minimal. Similar results were published by JEŽÍK et al. (2007), who stated that 72% of the annual increment was formed from the middle of May to the middle of July (DOY 135–191).

The analysis of the relationship between stem radial changes and environmental factors revealed that the characteristics influenced stem radial changes with different time lags. The only variable that was found

to have an immediate effect on daily stem radial changes was the soil water potential at a soil depth of 15 cm (Table 2). The characteristics with one-day time lag included in the multiple regression were the sum of global radiation and daily precipitation total. MÄKINEN et al. (2003) found similar results, when the correlation between radius change and precipitation during the previous day was higher ($r = 0.41$) than for the current day ($r = 0.21$). Similarly, JEŽÍK et al. (2007) showed strong positive responses of stem radial changes to precipitation during the preceding day.

The average air temperature with a time lag of two days had the greatest influence on daily stem radial changes (Table 2). This result was quite surprising because the studies from temperate ecosystems usually reveal that water availability had a dominant impact on stem radial growth (e.g. ORWIG, ABRAMS 1997, LÉBOURGEOIS et al. 2005, KÖCHER et al. 2012). Correlations between radius change and mean daily temperature are usually low, e.g. MÄKINEN et al. (2003) found the correlation coefficients $r = 0.08$, 0.00 and 0.03 for the current day and the two previous days, respectively. Our results indicate that the site is situated in a region that does not suffer from the lack of moisture (ŠKVARENINA et al. 2009).

Our results indicate that the sensitivity of stem radial changes of all three examined clones to the examined environmental factors was very similar (Table 2, Fig. 6). The analysis of variance revealed the differences between the individual years, reflecting differences in climatic conditions. GRYC et al. (2012) analysed the impact of drought stress on the regular cambium activity and wood formation in the stems of different clones of Norway spruce (*Picea abies* [L.] Karst). They found that the radial increment of some clones was affected less significantly in spite of the fact that all clones were exposed to the same drought intensity.

CONCLUSIONS

In our study, we investigated seasonal changes in stem circumference and the impact of climatic and soil moisture factors on the radial growth of Norway spruce clones in the Western Carpathian Mountains. We conclude that dendrometers are valuable tools that can provide us with information on the stem growth sensitivity to external factors. On the basis of the presented data measured by dendrometers we can state that the seasonal timing (beginning, culmination and termination) and the length of the main radial growth are driven by climatic conditions. However, small differences between individual clones and large differences between years show that it is diffi-

cult to predict the radial growth based on the genetic background due to the significant effects of environment and climate.

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References

- Bouriaud O., Leban J.M., Bert D., Deleuze C. (2005): Intra-annual variations in climate influence growth and wood density of Norway spruce. *Tree Physiology*, 25: 651–660.
- Bouriaud O., Popa I. (2009): Comparative dendroclimatic study of Scots pine, Norway spruce, and silver fir in the Vrancea Range, Eastern Carpathian Mountains. *Trees* 23: 95–106.
- Clausnitzer F., Kostner B., Schwärzel K., Bernhofer C. (2011): Relationships between canopy transpiration, atmospheric conditions and soil water availability – Analyses of long-term sap-flow measurements in an old Norway spruce forest at the Ore Mountains/Germany. *Agricultural and Forest Meteorology*, 151: 1023–1034.
- Čufar K., Prislan P., Gričar J. (2008a): Cambial activity and wood formation in beech (*Fagus sylvatica*) during the 2006 growth season. *Wood Research*, 53: 1–12.
- Deslauriers A., Rossi S., Anfondillo T. (2007): Dendrometer and intra-annual tree growth: What kind of information can be inferred? *Dendrochronologia*, 25: 113–124.
- Dillen S.Y., Storme V., Marron N., Bastien C., Neyrinck S., Steenackers M., Ceulemans R., Boerjan W. (2009): Genomic regions involved in productivity of two interspecific poplar families in Europe. 1. Stem height, circumference and volume. *Tree Genetics & Genomes*, 5: 147–164.
- Downes G., Beadle Ch., Worledge D. (1999): Daily stem growth patterns in irrigated *Eucalyptus globulus* and *E. nitens* in relation to climate. *Tree*, 14: 102–111.
- Drew D.M., Downes G.M., Grzeskowiak V., Naidoo T. (2009): Differences in daily stem size variation and growth in two hybrid eucalypt clones. *Trees*, 23: 585–595.
- Eriksson G. (1982): Ecological genetics of conifers in Sweden. *Silva Fennica*, 16: 149–156.
- IPCC (2001): Climate change 2001: the scientific basis. In: Contribution of Working Group I to the Third Assessment Report of the IPCC: Cambridge, Cambridge University Press: 83.
- Ge Z.M., Kellomäki S., Zhou X., Wang K.Y., Peltola H., Väisänen H., Strandman H. (2013): Effects of climate change on evapotranspiration and soil water availability in Norway spruce forests in southern Finland: an ecosystem model based approach. *Ecohydrology*, 6: 51–63.

- Gryc V., Hacura J., Vavrčik H., Urban J., Gebauer R. (2012): Monitoring of xylem formation in *Picea abies* under drought stress influence. *Dendrobiology*, 67: 15–24.
- Hyllen G. (1997): Genetic variation of wood density and its relationship with growth traits in young Norway spruce. *Silvae Genetica*, 46: 55–60.
- Ježík M., Blaženec M., Střelcová K. (2007): Intraseasonal stem circumference oscillations: their connection to weather course. In: Střelcová K., Škvarenina J., Blaženec M. (eds): *Bioclimatology and Natural Hazards*. International Scientific Conference. Poľana nad Detvou, Sept 17–20, 2007: [CD].
- Ježík M., Blaženec M., Letts M., Ditmarová L., Sitková Z., Střelcová K. (2014): Assessing seasonal drought stress response in Norway spruce (*Picea abies* (L.) Karst.) by monitoring stem circumference and sap flow. *Ecophysiology*, 8: 378–386.
- King G., Fonti P., Nievergelt D., Bntgen U., Frank D. (2013): Climatic drivers of hourly to yearly tree radius variations along a 6°C natural warming gradient. *Agricultural and Forest Meteorology*, 168: 36–46.
- Klein T., Rotenberg E., Cohen-Hilaleh E., Raz-Yaseef N., Tatarinov F., Preisler Y., Ogée J., Cohen S., Yakir D. (2014): Quantifying transpirable soil water and its relations to tree water use dynamics in a water-limited pine forest. *Ecophysiology*, 7: 409–419.
- Kmeř J., Ditmarová L., Kurjak D. (2008): Drought as stress factor and its role in spruce (*Picea abies* /L./ Karst) dieback. *Beskydy*, 1: 35–41.
- Knott R. (2004): Seasonal dynamics of the diameter increment of fir (*Abies alba* Mill.) and beech (*Fagus sylvatica* L.) in a mixed stand. *Journal of Forest Science*, 50: 149–160.
- Köcher P., Horna V., Leuschner Ch. (2012): Environmental control of daily stem growth patterns in five temperate broad-leaved tree species. *Tree Physiology*, 32: 1021–1032.
- Lapin M., Faško P., Kveták Š. (1988): Metodický predpis 3-09-1/1, Klimatické normály. Bratislava, SHMÚ: 25.
- Larcher W. (2003): *Physiological Plant Ecology – Ecophysiology and Stress Physiology of Functional Groups*. Berlin, Springer-Verlag: 514.
- Lebourgeois F., Bréda N., Ulrich E., Granier E. (2005): Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). *Trees*, 19: 385–401.
- Mayer P., Prins K. (2003): State of Europe's Forests 2003. The MCPFE Report on Sustainable Forest Management in Europe. Horn, Ferdinand Berger & Söhne GmbH: 114.
- Mäkinen H., Nojd P., Saranpää P. (2003): Seasonal changes in stem radius and production of new tracheids in Norway spruce. *Tree Physiology*, 23: 959–968.
- Mistrík I., Ješko T., Repčák M., Masarovičová E., Gašparíková O. (2002): Fyziológia stresu. In: Masarovičová E., Repčák M. et al. (eds): *Fyziológia rastlín*. Bratislava, Univerzita Komenského: 267–283.
- Oberhuber W., Gruber A. (2010): Climatic influences on intra-annual stem radial increment of *Pinus sylvestris* (L.) exposed to drought. *Trees*, 24: 887–898.
- Orwig D.A., Abrams M.D. (1997): Variation in radial growth responses to drought among species, site, and canopy strata. *Trees*, 11: 474–484.
- Panshin A.J., De Zeeuw C. (1980): *Textbook of Wood Technology*. New York, McGraw-Hill: 722.
- Sevanto S., Suni T., Pumpanen J., Grönholm T., Kolari P., Nikinmaa E., Hari P., Vesala T. (2006): Wintertime photosynthesis and water uptake in a boreal forest. *Tree Physiology*, 26: 749–757.
- Schmitt U., Möller R., Eckstein D. (2000): Seasonal wood formation dynamics of beech (*Fagus sylvatica* L.) and black locust (*Robinia pseudoacacia* L.) as determined by the “pinning” technique. *Journal of Applied Botany*, 74: 10–16.
- Schmidt-Vogt H. (1978): Genetics of *Picea abies* (L.) Karst. *Annales Forestales*, 7/5: 147–186.
- Sonesson J., Eriksson G. (2003): Genetic variation in drought tolerance in *Picea abies* seedlings and its relationship to growth in controlled and field environments. *Scandinavian Journal of Forest Research*, 18: 7–18.
- Soulé P.T. (2011): Changing climate atmospheric composition and radial tree growth in a spruce-fir ecosystem on Grandfather Mountain, North Carolina. *Natural Areas Journal*, 31: 65–74.
- Strmeň S. (2004): Stav autovegetatívneho smrekového porastu 11 rokov po výsadbe v imisiách zasiahnutej oblasti Kysúc. *Forestry Journal*, 50: 41–52.
- Škvarenina J., Tomlain J., Hrvol J., Škvareninová J., Nejedlík P. (2009): Progress in dryness and wetness parameters in altitudinal vegetation stages of West Carpathians: Time-series analysis 1951–2007. *Quarterly Journal of the Hungarian Meteorological Service*, 113: 47–54.
- Vieira J., Rossi S., Campelo F., Freitas H., Nabais C. (2013): Seasonal and daily cycles of stem radial variation of *Pinus pinaster* in a drought-prone environment. *Agricultural and Forest Meteorology*, 180: 173–181.
- Vitas A. (2011): Seasonal growth variation of pine, spruce, and birch recorded by band dendrometers in NE Lithuania. *Baltic Forestry*, 17: 197–204.
- Volland-Voigt F., Brauning A., Ganzhi O., Peters T., Maza H. (2011): Radial stem variations of *Tabebuia chrysantha* (Bignoniaceae) in different tropical forest ecosystems of southern Ecuador. *Trees*, 25: 39–48.
- Zweifel R., Häsler R. (2001): Dynamics of water storage in mature subalpine *Picea abies*: temporal and spatial patterns of change in stem radius. *Tree Physiology*, 21: 561–569.
- Zweifel R., Item H., Häsler R. (2000): Stem radius changes and their relation to stored water in stems of young Norway spruce trees. *Trees*, 15: 50–57.

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