



Inter- and intra-annual dynamics of height increment in young beech and spruce stands in relation to tree size and weather conditions

Vnútro- a medziročná dynamika výškového prírastku v mladých porastoch buka a smreka vo vzťahu k veľkosti stromu a poveternostným podmienkam

Bohdan Konôpka^{1,2*}, Jozef Pajčík^{1,2}, Michal Bošela^{1,2}, Tomáš Hlásny^{1,2}, Zuzana Sitková¹

¹National Forest Centre - Forest Research Institute Zvolen, T. G. Masaryka 2175/22, SK – 960 92 Zvolen, Slovakia

²Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129, CZ – 165 21 Praha 6 - Suchbátka, Czech Republic

Abstract

We investigated the seasonal dynamics of height increment, as well as total annual height increment, in 2009–2013 on young stands of beech and spruce grown at the same site. The results showed that the inter-annual dynamics of basic stand characteristics, especially tree density, were more obvious in spruce than in beech stands. Much higher tree mortality in spruce was explained by a lower light intensity under the spruce stand canopy and higher tolerance of beech to shade. Large interspecific differences were also found in the timing of height increment. Specifically, the height increment of beech trees started earlier than those of spruce. Moreover, the terminal growth was longer in spruce (nearly 70 days) compared to beech (about 45 days). The comparisons between the courses of the height increment and the ambient factors suggested that global radiation played a principal role. In the beech stand, the maximum height increment rate occurred during the same days as the maximal global radiation in 2009 and 2011, while a decline of the height increment occurred simultaneously with a depression in global radiation in 2012. As for the spruce stand, its one-peak maxima in height increment were related to the maximum of global radiation in 2009 and in 2012. On the other hand, double-peak courses of height increment in 2010 and 2011 may have been related to sudden declines in global radiation. Interspecific differences in height increment timing might play a certain role in cases of unfavourable weather conditions, e.g. drought episodes in the middle part of the growing season when the height increment would be accomplished in beech but would still be ongoing in spruce.

Keywords: *Fagus sylvatica*; *Picea abies*; terminal growth seasonality; global radiation; precipitation

Abstrakt

Počas rokov 2009–2013 sme sledovali sezónnu dynamiku výškového prírastku, ako aj celoročný výškový prírastok v bukových a smrekových mladinách rastúcich na totožnom stanovišti. Výsledky naznačili, že medziročné zmeny základných porastových charakteristík, a to najmä hustota porastu, boli výraznejšie v smrečine než v bučine. Omnoho vyššia stromová mortalita v smrečine sa vysvetlila nižšou intenzitou svetla pod koronovou vrstvou smrekov, resp. vyššou toleranciou buka na zatienie. Veľké medzidruhové rozdiely sa zaznamenali v „načasovaní“ výškového prírastku. Konkrétne výškový prírastok bukov začal každoročne skôr ako výškový prírastok smrekov. Ďalej, terminál smrekov rástol dlhšie (približne 70 dní) v porovnaní s bukmi (45 dní). Porovnanie priebehov výškových prírastkov vzhľadom na prostredie naznačilo, že principiálny vplyv mala globálna radiácia. V bučine bola maximálna intenzita výškového prírastku počas dní s maximálnou úrovňou globálnej radiácie, a to v rokoch 2009 a 2011, zároveň pokles intenzity sa objavil simultánne s poklesom globálnej radiácie počas roku 2012. V smrečine intenzita výškového prírastku predstavovala jednovrcholovú krivku – s najvyššou intenzitou prírastku v dňoch maximálnych hodnôt globálnej radiácie počas 2009 a 2012. Na druhej strane sa zaznamenal dvojrýcholový výskyt maxim intenzity výškového prírastku smrekov v 2010 a 2011. Tento jav súvisel s dočasným poklesom globálnej radiácie v týchto rokoch. Medzidruhové rozdiely v načasovaní výškového prírastku môžu mať relevanciu v prípade výskytu nepriaznivých poveternostných podmienok. Napríklad pri epizódach sucha v polovici vegetačného obdobia, keďže výškový prírastok je vtedy už ukončený pri bukoch avšak na smrekoch ešte prebieha.

Kľúčové slová: *Fagus sylvatica*; *Picea abies*; sezónnosť prírastku na termináli; globálna radiácia; zrážky

1. Introduction

Height increments in most tree species, including the genera of *Fagus* and *Picea*, result from expansion of the terminal bud on the main stem (Kozłowski & Pallardy 1997). Tree height increment, as well as plant growth in general, is determined by individual heredity and environmental conditions. Kozłowski (1964) explained that the environmental regime controls the extent to which the hereditary potential of plants is expressed. As for the environmental effects on

tree height, three groups by origin can be considered: from climate, soil and plant (tree) competition. Carter et al. (1988) defined the effects of climate on plants as direct (especially radiation, temperature and water availability from soil) or as indirect but climate-sensitive (mainly nutrient availability, interference of pests). Soil conditions influence tree growth, including height increment, to a large part, and they are related to the prevailing chemical and physical properties of the ground (Lukac & Godbold 2011). An intensive influ-

*Corresponding author. Bohdan Konôpka, e-mail: bkonopka@nlcsk.org, phone: +421 45 531 43 23

ence of tree competition on height increment was found in young Norway spruce (*Picea abies*) stands originating from natural regeneration (Šebeň et al. 2013). A reduced or nearly inhibited height increment was observed in juvenile individuals of beech and spruce grown under the parent forest stand, which was caused predominantly by light availability (Šamonil & Vrška 2008; Jarčuška & Barna 2011). The tree height increment in dense stands is probably regulated not only by above-ground competition (for light and space) but also by below-ground competition (for water, nutrients and space); however, knowledge on below-ground interactions is still scarce (see, for example, Rewald & Leuschner 2009) and provide an opportunity for future scientific activities.

In fact, a relatively large number of studies have dealt with inter-annual variation of tree height increments especially with regard to weather conditions (e.g. Salminen & Jalkanen 2004; Lindholm et al. 2011; Wang et al. 2012; Šebeň et al., 2013). On the other hand, we are missing detailed knowledge of the seasonal dynamics of height increment and an exact study explaining the factors governing the variability of intra-annual height growth. Precise measurement of the seasonal course of tree height increments in comparison with seasonal stem radial increments is technically more complicated. This kind of measurement is particularly difficult for high trees since the terminal is far from the ground level (physically inaccessible), and remote measurements (e.g. by a laser hypsometer) do not produce satisfactorily precise estimates. Hence, we could find only a few papers (Dimock 1964; Kinberley & Richardson 2004) related to the seasonal dynamics of tree height increments. Moreover, the existing papers did not consider the relationship between tree competition and intra-annual elongation of the terminal shoot.

Considering the information obtained from the previous papers, we decided to study the height increment in two forest tree species – European beech and Norway spruce – with the primary aim of elucidating interspecific differences. A further aim was to describe the main reasons causing inter-annual and intra-annual variability of height increment. We considered two principal groups of influences: tree competition in stands (expressed by relative tree height) and meteorological factors (air temperature, global radiation, precipitation).

2. Materials and methods

2.1. Site and stands description

Our studies were conducted at the site “Vrchslatina” (see also Konôpka et al. 2013). The site is situated in the geomorphological unit of Veporské vrchy Mts., subunit Sihlianska plateau, which is composed mainly of porphyric granodiorites, biotite tonalites and granites. Cambisols were developed from this parent material. The soil properties at the research site are favourable. The soil is classified as Cambisol (Humic, Eutric). The textural class of the fine earth fraction is qualified as sandy loam. Though the rock fragment content is relatively high (about 30–35% volume in the whole assessed soil profile), almost all of the rock fragments are in the fine gravel fraction (0.2–0.6 cm) and so this does not have a negative influence on the soil properties. The soil pH is slightly acidic. The values of pH measured in hydrosuspension were between 5.1 and 5.4, while the values measured in CaCl₂

extract were between 4.3 and 4.6. The content of soil organic carbon (SOC) is high and above average for forest soils in Slovakia. Research activities took place in forest complexes composed exclusively of beech or spruce. The site is forested by similar-aged stands originating from natural regeneration from around 1995 under a sparse tall forest. The patches of beech and spruce utilised in this research were directly neighbouring and were each approximately 0.7 ha in size making up compact clumps (groups of trees) of varying density with a few scattered gaps dominated by *Calamagrostis epigejos* [L.].

2.2. Tree and meteorological measurements

In April 2009, we established five plots in the beech stand and also five plots in the spruce stand. The plots were circular and placed so as to avoid atypical spots (e.g. gaps, stand ages). The plots had a radius of between 0.7 and 1.0 m – their size depended on stand density and was adjusted to include approximately 30 individuals of beech or spruce. Every year, specifically in 2009–2013, we measured the basic characteristics of the trees including: diameter at stem base (d_0), diameter at breast height ($d_{1.3}$) and tree height. The measurements were done outside the growing season (either very early spring or late autumn). The diameters were measured in two perpendicular directions by means of digital callipers with a precision of 0.1 mm on the stem base for all trees, and 130 cm from the ground level for those that exceeded this height. Tree heights were measured by a wooden meter with a precision of 1 cm for trees up to a height of 2 m, and for higher ones with a precision of 5 cm. Mean diameters, mean heights and mean stem volume were calculated as weighted arithmetic means from plot average numbers weighted by plot sizes. To calculate the mean height, we used the Lorey procedure. To express the stem volume of trees, the same approach as in our previous paper was used (Pajtík et al. 2011). Subsequently, mean stem volume was calculated as an average from the stem volumes of all trees on the plots. Every year, the trees were categorised according to their height. Specifically, we defined four height classes as follows:

- A class – tree height 0–25% of the tallest tree in the stand (quasi suppressed),
- B class – tree height 26–50% of the tallest tree in the stand (quasi subdominant),
- C class – tree height 51–75% of the tallest tree in the stand (quasi co-dominant),
- D class – tree height over 75% of the tallest tree in the stand (quasi dominant).

Moreover, 40 individuals of beech and 40 of spruce were selected for intra-annual repetitive height measurements within the specific years. The trees were selected to cover the entire interval of height recorded in the stand with 10 individuals for each height class (as explained above). To record the seasonality of height increment, the length of the current-year terminal was measured repetitively on the trees about ten times during its growth. The terminal measurements were done by a wooden meter with a precision of 1 cm on bent trees in the years 2009–2012. The measurement was not performed in 2013 because of difficulty in bending tree stems in the D-height class, and therefore we decided to also not measure the trees in the A, B and C classes.

Besides tree measurements, since the spring of 2009 we conducted meteorological monitoring using an automatic weather station placed in an open area close to the research stands. Air temperature ($^{\circ}\text{C}$) and relative humidity (%) were measured at 10-minute intervals using the integrated datalogger Minikin TH (EMS Brno, Czech Republic) covered by a radiation shield. Global radiation ($\text{W}\cdot\text{m}^{-2}$) was measured at 10-minute intervals by the smart sensor Minikin RT (EMS Brno, CZ). Data were stored as 30-minute averages. Precipitation totals were recorded during every rainfall event using the datalogger MicroLog ER (EMS Brno, CZ) and by a tipping bucket rain-gauge (MetOne 370, USA).

All mathematical operations and statistical analyses were performed in Statistica 10.0 software. Inter-annual differences in tree height increment in regard to height group were analysed by one-way ANOVA and separated by the LSD test. Since results on tree height originate from two different groups of trees, we will distinguish them in the subsequent text: results from the five circle plots will be referred to as “circle plots” (represents data for 2009–2013), while results from 40 individuals of each species are referred to as “selected trees” (2009–2012).

3. Results and discussion

3.1. Inter-annual changes in height increment

In 2009, the young beech and spruce stands were similar in most characteristics, namely number of trees, mean diameter and mean stem volume. On the other hand, certain differences existed between mean stand heights. The stands of both beech and spruce manifested large inter-annual changes in basic stand characteristics (Table 1). As for the number of trees, the decrease between the years of 2009 and 2013 was much sharper in spruce, specifically from 176 thousands

(thds hereinafter) to 48 thds trees per ha than in beech (from 157 thds to 110 thds trees per ha). This phenomenon is important because a decreasing number of trees (mortality appeared mainly in smaller trees) also influenced other stand characteristics such as average tree size expressed by height, diameter or stem volume. Thus, while interspecific differences were small in the case of mean stand height increment, large interspecific differences were recorded for dynamics of mean stem diameter (twofold in favour of spruce) and mean stem volume (threefold in favour of spruce).

Stand development under a high tree density (competition stress) between 2009 and 2013 caused dramatic changes in height frequency distribution in both stands (Fig. 1 and 2). Larger changes were found in beech stands, since many trees shifted to height categories over 4 m. At the same time, smaller trees (under 1 m) were more able to persist in the beech stand than in the spruce stand. The results showed much higher mortality of small trees in the spruce stand than in the beech stand between 2009 and 2013 (Tables 2 and 3). The results show that while 27.94% of all beeches recorded in 2009 died during 2009–2013, the mortality in spruce was as high as 73.50%. In fact, nearly all spruces that were categorised into the A–height class died in the period 2009–2013. On the other hand, about one-third of beech categorised into the A–height class in 2009 survived, and the rest died till autumn 2013. We found very different proportions of trees in the specific height classes between beech and spruce stands as early as in the beginning of the experiment (Tables 2 and 3, column “Together”). Specifically, the largest differences were found between the A classes (9.01% and 17.50% in beech and spruce, respectively) and especially between the D classes (36.93% and 13.50% in beech and spruce, respectively).

Further, we analysed inter-annual changes in absolute and relative numbers of trees in the height classes for both

Table 1. Basic stand characteristics for the beech and spruce stands in 2009 and 2013 (data from the circle plots).

Stand characteristics	Year 2009		Year 2013		Differences 2013–2009	
	Beech	Spruce	Beech	Spruce	Beech	Spruce
Number of trees [thds. $\cdot\text{ha}^{-1}$]	157	176	110	48	–47	–128
Lorey's mean height [cm]	225	172	485	423	260	251
Mean diameter d_0 [cm]	1.89	1.88	3.17	4.68	1.28	2.80
Mean stem volume [cm^3]	233	225	964	2437	731	2212

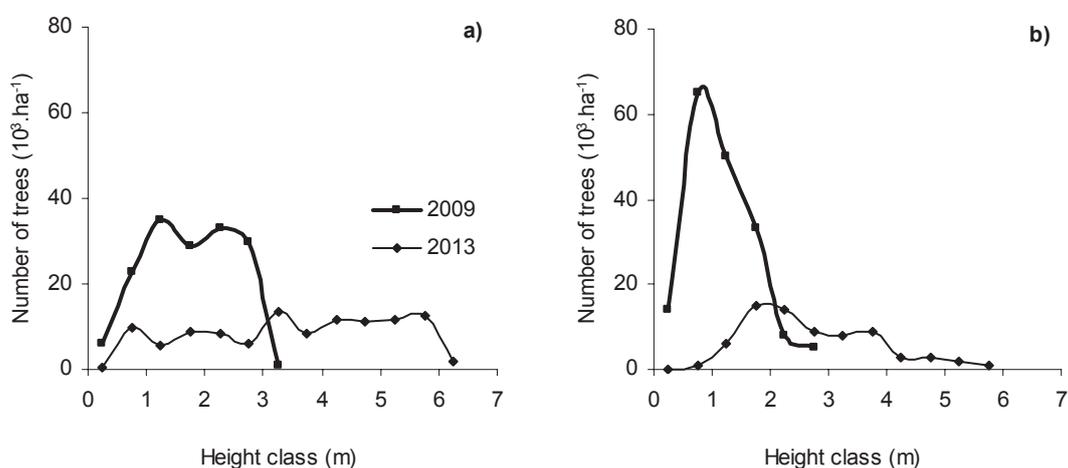


Fig. 1. Tree height frequency in the beech (a) and spruce (b) stand in the years 2009 and 2013 (data from the circle plots).

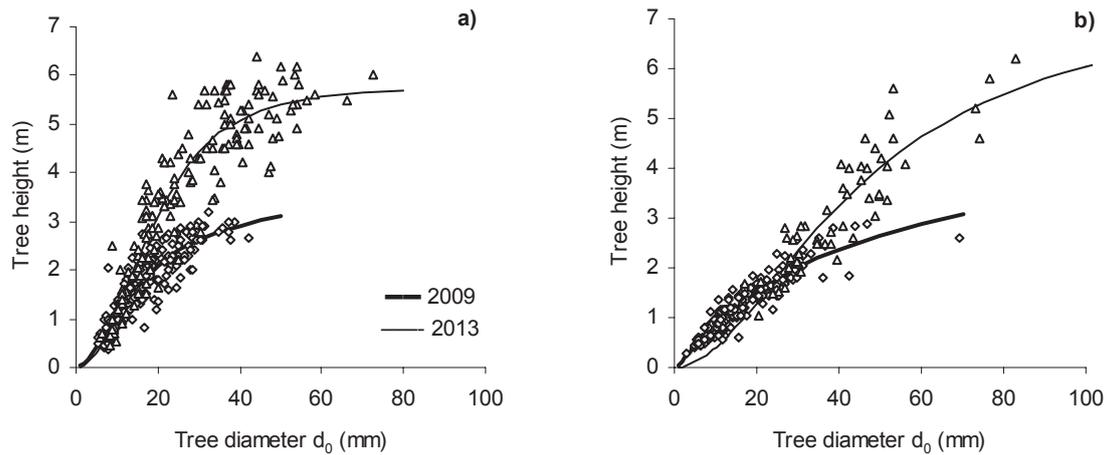


Fig. 2. Height curves for beech (a) and spruce (b) stands in the years 2009 and 2013 (data from the circle plots).

Table 2. Tree shifts between the height classes in the beech stand in the period 2009–2013. Percentage of the total number of trees present on the plots in 2009 is shown (data from the circle plots).

Shifts among classes	A	B	C	D	Dead	Together
A	3.15	0.00	0.00	0.00	5.86	9.01
B	6.76	1.80	0.00	0.00	15.77	24.33
C	0.00	11.71	11.26	1.35	5.41	29.73
D	0.00	0.45	7.66	27.92	0.90	36.93
Sum	9.91	13.96	18.92	29.27	27.94	100.00

Table 3. Tree shifts between the height classes in the spruce stand in the period 2009–2013. Percentage of the total number of trees present on the plots in 2009 is shown (data from the circle plots).

Shifts among classes	A	B	C	D	Dead	Together
A	0.00	0.00	0.00	0.00	17.50	17.50
B	0.50	0.50	0.00	0.00	40.50	41.50
C	0.00	11.00	1.50	0.00	15.00	27.50
D	0.00	0.50	6.50	6.00	0.50	13.50
Sum	0.50	12.00	8.00	6.00	73.50	100.00

tree species (Fig. 3 and 4). The number of trees decreased gradually in all height classes in both tree species except for the A-height class in the beech stand (Fig. 3a, b). A slight increase of beeches in the A-height class was caused by a larger shift of trees from other height classes to the A class than mortality of trees in this class. Mortality of trees, as well as shifts of trees among the height classes, during the period 2009–2013 modified the proportion of trees in the particular height classes compared to the total tree number (Fig. 4a, b). As for the beech stand, increased contributions of trees in the A- and D-height classes were recorded. While a decreased contribution was typical for the B-height group, the contribution of the C-height group manifested inter-annual fluctuation but statuses in 2009 and 2013 were nearly equal. The relative share of trees in the height classes changed during the years of observation more dramatically in spruce than in beech. In the spruce stand, sharp increases were found in the C- and D-height classes and decreases in the A- and B-height classes.

As a final step of our analyses on inter-annual height increment fluctuation, we tested annual height increments within the height classes for both forest stands (Tables 4 and 5). The results indicated that, in both stands, the shortest

increment for the A-height class was recorded in 2012, which might be related to enhanced competition stress due to increasing stand density. As for the B-height classes, the longest height increments in both stands were found in 2009, which also might be linked to canopy development (least closed in 2009). As for the height classes C and D, inter-annual differences were very small in both stands. An exception was found in the spruce stand: the height class C had a significantly larger increment in 2010 and 2011 than in 2012.

Summarising all the results achieved, we assume that inter-annual differences in height increment were mostly related to stand development, specifically canopy density, which determines competition pressure on individual trees. Higher tree mortality as well as inter-annual changes in height frequency structure (especially on the account of small trees) were recorded in the spruce than in the beech stand. This phenomenon is most probably related to lower light intensity under the spruce canopy and higher shade tolerance of beech (see for example, Schmidt-Vogt 1977; Barna et al. 2011). In general, beech is able to persist under light intensity equalling 1–2% of the above-canopy light level, and optimum growth conditions are under 30–40% of the above-canopy light (Aussenac 2000; Ammer 2003; Kunstler et al. 2005).

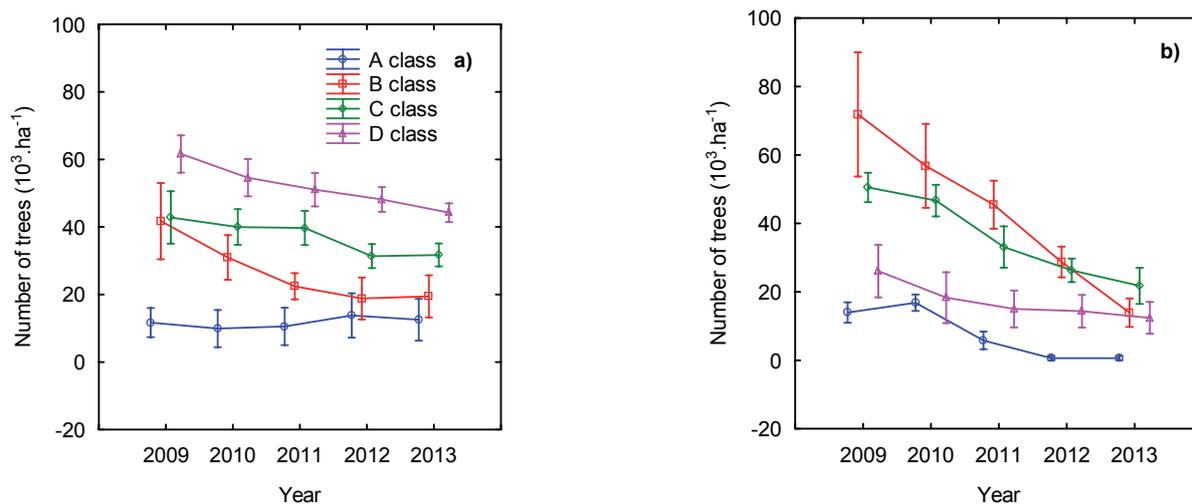


Fig. 3. Hectare number of beeches (a) and spruces (b) of the specific height classes in the years 2009–2013 (data from the circle plots).

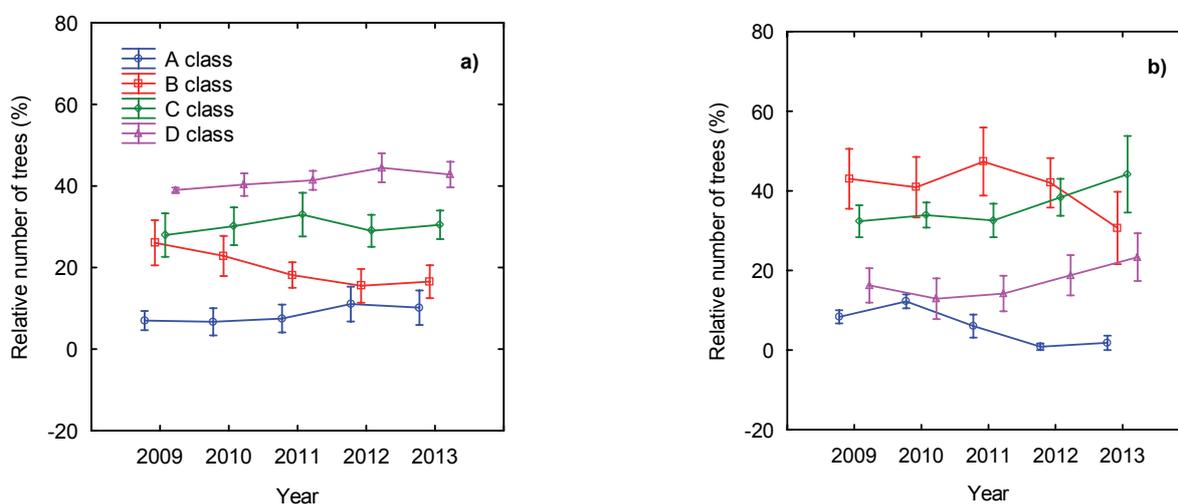


Fig. 4. Relative contribution of beeches (a) and spruces (b) of the specific height classes in the years 2009–2013 (data from the circle plots).

Table 4. Annual height increment (cm) in the beech with regard to the height classes for the years 2009–2012. Mean values and standard deviations are shown (data from the selected trees).

Class versus year	2009	2010	2011	2012
A	8.0 ± 9.4 ^a	2.5 ± 4.3 ^{ab}	2.4 ± 5.8 ^{ab}	0.7 ± 1.6 ^b
B	28.3 ± 15.5 ^a	11.2 ± 12.5 ^{ab}	9.8 ± 19.1 ^b	24.2 ± 22.2 ^{ab}
C	49.9 ± 9.3 ^a	46.5 ± 15.7 ^a	45.6 ± 21.2 ^a	47.3 ± 20.0 ^a
D	54.9 ± 8.3 ^a	48.0 ± 8.2 ^a	55.8 ± 17.5 ^a	51.9 ± 9.9 ^a

Note: the different letters indicate significant differences among the years (LSD test, $\alpha = 0.05$).

Table 5. Annual height increment (cm) in the spruce with regard to the height classes for the years 2009–2012. Mean values and standard deviations for the specific years are shown (data from the selected trees).

Class versus year	2009	2010	2011	2012
A	4.6 ± 4.1 ^{ab}	6.9 ± 4.5 ^a	2.1 ± 2.5 ^b	1.9 ± 3.6 ^b
B	19.8 ± 8.2 ^a	12.0 ± 7.4 ^b	10.6 ± 10.1 ^b	11.6 ± 7.4 ^b
C	34.5 ± 9.6 ^{ab}	39.2 ± 11.0 ^a	42.4 ± 11.1 ^a	28.5 ± 9.3 ^b
D	58.4 ± 11.3 ^a	53.8 ± 11.6 ^a	47.6 ± 10.2 ^a	47.1 ± 8.1 ^a

Note: the different letters indicate significant differences among the years (LSD test, $\alpha = 0.05$).

Reynolds & Frochot (2003) found, in European conditions, that average light intensity under a mature beech stand was approximately 5% of the above-canopy light level.

As for the influence of weather conditions on the inter-annual fluctuation of height increment, we could not clearly prove any relationship. The main reason was the short duration of the experiment and the non-uniform responses of trees with different sizes (height classes). A clear effect of air temperature on current-year height increment was shown by a variety of papers that usually refer to early summer weeks of the previous year (e.g. Salminen & Jalkanen 2005; Lindholm et al. 2009) or summer weeks of the current year (Gamache & Payette 2004; Salmine & Jalkanen 2004), eventually summer temperatures in both previous and current years (Wang et al. 2012). These interactions might be related to the fact that shoot extension of most tree species is a 2-year-process involving firstly the formation of terminal buds and then shoot elongation itself (Kozłowski 1964).

3.2. Seasonal dynamics of height increment

Seasonal dynamics were primarily analysed with regard to the height classes. For this purpose, the cumulative height

increments between the two measurements are expressed as a percentage of the total annual increment (Fig. 5a, b). In most years, for the spruce stand, height increment in the A-height class was delayed compared to those found in the other height classes. On the other hand, this phenomenon was not clear in the beech stand (differences between height classes were not significant). Interspecific differences in height increment timing between the beech and spruce stands can be seen from comparison of all 40 measured trees regardless of tree size (Fig. 6a, b). Clearly, height increments started earlier in beech (between the 120th and 125th day of the current year, i.e. the very beginning of May) than in spruce (135–140th day, i.e. the middle of May). Moreover, the terminals grew for longer in spruce (nearly 70 days) than in beech (about 45 days). Thus, the height increments finished much earlier in beech (usually between the 165th and 170th day, i.e. the middle of June) than in spruce (between the 205th and 210th day, i.e. the second half of July).

We also analysed the seasonal dynamics of height increments in beech and spruce as expressed by the percentage of the increment between the two measurements for the current-year total increment (Fig. 7a, b). This kind of description illustrates the height increment rate in a certain part of the growing season. In fact, the maximum height increment

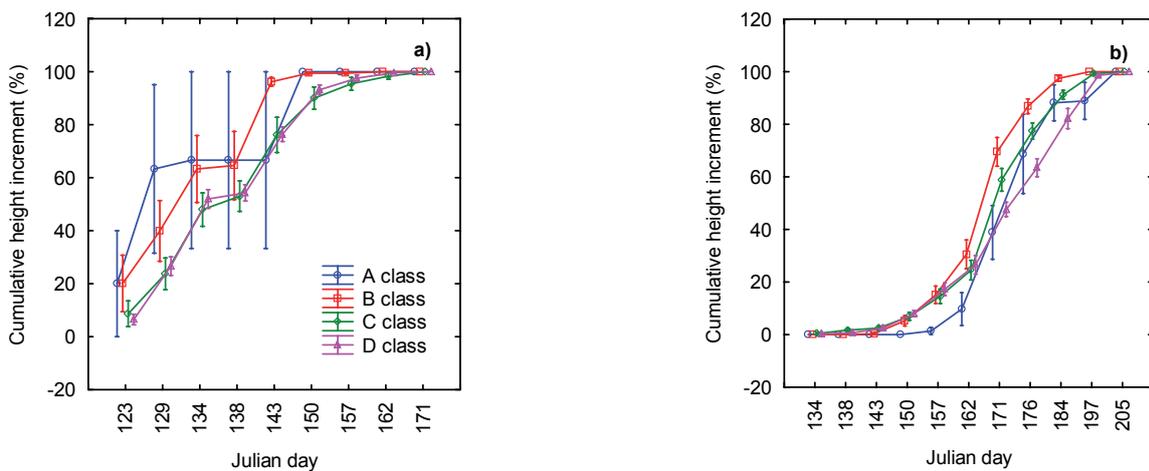


Fig. 5. Seasonal dynamics of cumulative height increment in beech (a) and spruce (b) with regard to the specific height classes in 2012 expressed as a percentage (data from the selected trees). The Julian days shown on the x-axis are dates of the increment measurements.

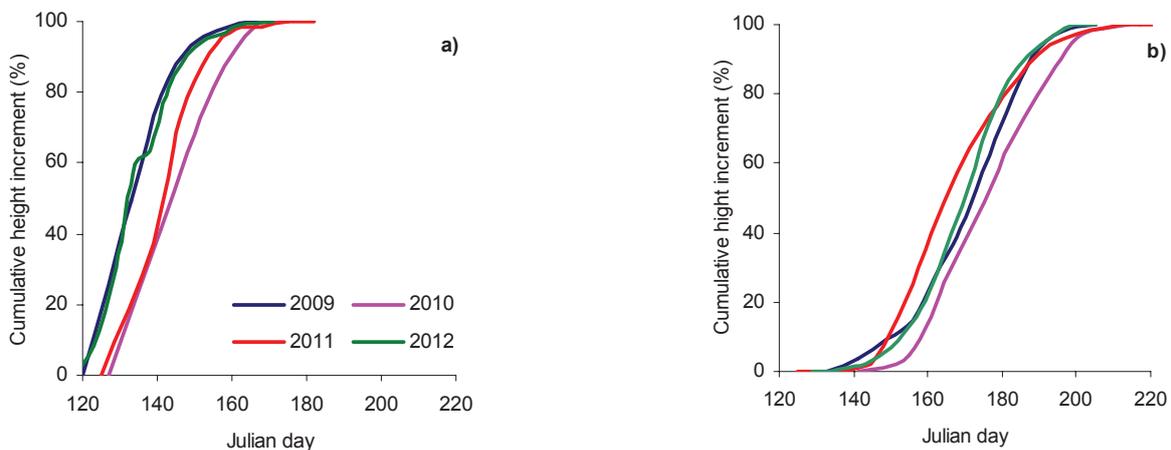


Fig. 6. Seasonal dynamics of cumulative height increment in beech (a) and spruce (b) regardless of the height classes in the years of 2009–2013 expressed as a percentage (data from the selected trees).

rate varied greatly between the years. For instance, in 2012 the maximum height increment of beech occurred on the ca. 135th day of the current year, while in 2010 the maximum increment was recorded about 15 days later. Similarly, in spruce, in 2011 the maximum height increment occurred on the ca. 160th day of the current year, while in 2009 the height increment reached its maximum rate about 20 days later. Moreover, an interesting finding is that the maximum rate of height increment in some years manifested as one-peak courses, while in other years it was a double-peaked curve.

Since we recorded inter-annual variability in the beginning of terminal growth in both beech and spruce, as well as in its duration and seasonal courses, we assumed that these differences would be related to weather conditions of the current year. We compared annual courses of height increments (Fig. 7a, b) with courses of global radiation (expressed as the sum of the radiation between two measurements of the height increment; Fig. 7c) and precipitation (similarly, expressed as the sum of the precipitations between two measurements of the height increment; Fig. 7d). We excluded analyses on air temperature because they closely coincide with global radiation. The comparisons between the courses of the height increment and the weather variables suggested that global radiation played a significant role. For example, in the beech stand, the maximum height increment rate occurred during the same days as the maximum global radiation in 2009 (135th day) and 2011 (140th day), while a decline of the height increment occurred simultaneously with a depression in the global radiation in 2012 (ca. 140th day). As for the spruce stand, the one-peak maxima in height increment were related to the maxima of global radiation in 2009 (ca. 180th day) and in 2012 (ca. 170th day). On the other hand, double-peaked courses of the height increment in 2011 and 2012 might be related to the sudden declines in global radiation (on the ca. 180th day in both years). As for the influence of precipitation on height increment, we assume that it would not be important because of abundant water resources in the soil during the first half of the growing season, originating mostly from snow cover. Dry periods (low soil moisture) may occur in this altitude, usually after the 220th day, i.e. after the period of terminal growth (see also Priwitz et al. 2013). However, a certain influence of height growth rate by precipitation could be assumed due to the coincidence of peaks in both characteristics in spruce stands during 2009 (on the ca. 185th day).

The results show that global radiation in the current year regulates intensity of height increment in both beech and spruce. A sudden decline of global radiation caused a rapid response of the height increment in the form of a reduction, and thus the annual height increment course occurred as a double-peaked curve. In fact, the relationship between the growth of juvenile beech and light conditions highlights a number of studies previously conducted under control (Tognetti et al. 1997) or natural (Collet et al. 2001; Collet & Chenost 2006) conditions. We suppose that while the course of the height increment intensity in beech and spruce is regulated by the development of current-year temperature (or global radiation), the final length of the terminal increment is possibly the result of temperatures in both the previous and current years (see also Wang et al. 2012). Moreover, we can assume that the height increment rate, as well as the

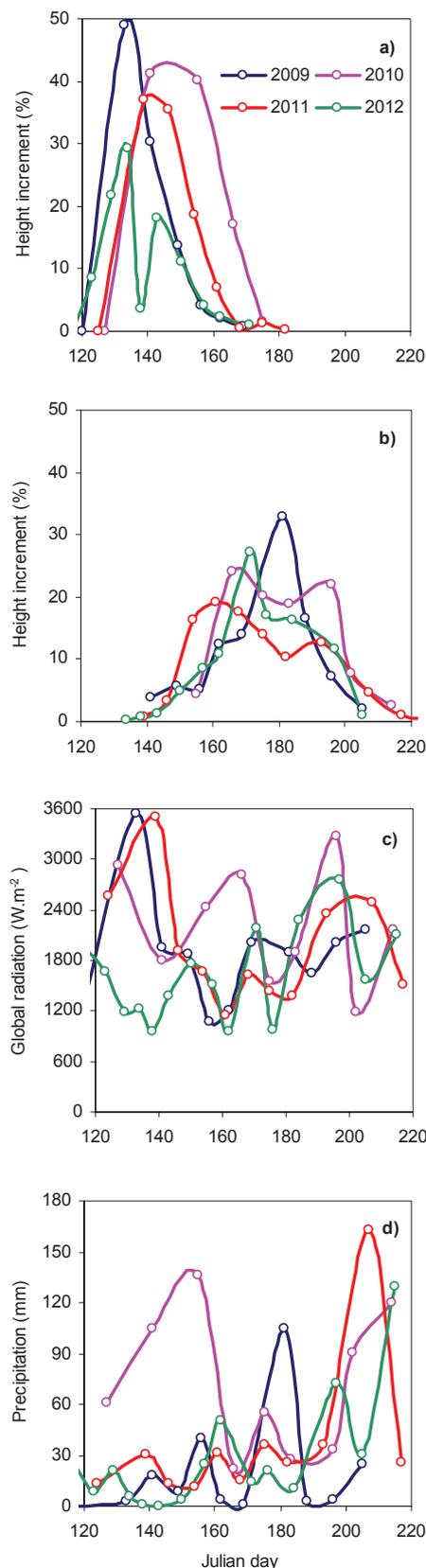


Fig. 7. Seasonal dynamics of height increment in beech (a) and spruce (b) in the years 2009–2013 expressed as a percentage (data from the selected trees) in comparison with the courses of global radiation (c) and precipitation (d).

total annual increment, of spruce could be influenced by the current year precipitation, especially in the years with little snow cover at the end of winter and a lack of precipitation in spring. Some indication of this kind of phenomenon was found in June 2009 when the height increment of spruces was delayed, most probably due to the lack of precipitation and then suddenly stimulated due to the rewetted soil. In general, spruce in comparison with beech starts with a later height increment and, at the same time, is a more water-demanding species. Thus, soil moisture may be more limiting for terminal elongation in spruce than in beech. This is in agreement with the stem diameter increment since Bošela et al. (2013) proved at the same site that, while stem thickening in beech was governed more by temperature, thickening in spruce was related mainly to the course of precipitation.

4. Conclusions

Our results show contrasting developments between young beech and spruce stands in the years 2009–2013. Specifically, much higher tree mortality occurred in the spruce stand than in the beech stand. This may be related to lower light intensity under the spruce stand canopy (related to crown densities and tree height structure) and a higher tolerance of beech to shade. The height increment of both beech and spruce varied between the particular years but inter-annual differences were not uniform in all height groups. We found large difference between beech and spruce in timing and duration of height increment. Specifically, the beech started earlier and the time of growth was shorter than in the spruce. The course of height growth intensity was related to global radiation for both species. A sudden decrease of global radiation caused a double-peaked course of the height increment. We assume that interspecific differences in height increment timing (concurrent with the development of foliage) can play a role during unfavourable conditions, e.g. drought episodes in the middle of the growing season.

Acknowledgements

This work was supported by the Slovak Research and Development Agency under contracts no. APVV-0268-10 and APVV-0111-10, and also partly by the Ministry of Agriculture of the Czech Republic under contract No. QJ1220316.

References

- Ammer, C., 2003: Growth and biomass partitioning of *Fagus sylvatica* L. and *Quercus robur* L. seedlings in response to shading and small changes in the R/FR-ratio of radiation. *Annals of Forest Science* 60:163–171.
- Aussenac, G., 2000: Interaction between forest stands and microclimate: ecophysiological aspects and consequences for silviculture, *Annals of Forest Science* 57:287–301.
- Barna, M., Kulfan, J., Bublinec, E., 2011: Buk a bukové ekosystémy Slovenska. Beech and Beech Ecosystems of Slovakia. VEDA, Bratislava, 636 p.
- Bošela, M., Pajčík, J., Konôpka, B., Šebeň, V., Vida T., 2013: Modelling effects of weather conditions on seasonal dynamics of the stem circumference increment in a mixed stand of Norway spruce and European beech. *Lesnícky časopis - Forestry Journal* 59:180–188.
- Carter, T. R., Konijn, N., Watts, R., 1988: The choice of first-order impact model. In: Parry, M. L., Carter, T. R., Konijn, N. T.: The impact of climatic variations in agriculture. Kluwer, Dordrecht, p. 97–123.
- Collet, C., Chenost, C., 2006: Using competition and light estimates to predict diameter and height growth of naturally regenerated beech seedlings growing under changing canopy conditions. *Forestry* 79:489–502.
- Collet, C., Lanter, O., Pardos, M., 2001: Effects of canopy opening on height and diameter growth in naturally regenerated beech seedlings. *Annals of Forest Science* 58:127–134.
- Dimock, E. J., 1964: Simultaneous variations in seasonal height and radial growth of young Douglas-fir. *Journal of Forestry* 62:252–255.
- Gamache, I., Payette, S., 2004: Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada. *Journal of Ecology* 92:835–745.
- Jarčuška, B., Barna, M., 2011: Influence of light availability on height growth of naturally regenerated beech with different growth histories. *Austrian Journal of Forest Science* 128:53–65.
- Kinberley, M. O., Richardson, B., 2004: Importance of seasonal growth patterns in modeling interactions between radiate pine and some common weed species. *Canadian Journal of Forest Research* 34:184–194.
- Konôpka, B., Pajčík, J., Malová, M., 2013: Fine root standing stock and production in young beech and spruce stands. *Lesnícky časopis - Forestry Journal* 59:163–171.
- Konôpka, B., Pajčík, J., Šebeň, V., Bošela, M., Máliš, F., Priwitzer, T. et al., 2013: The Research Site Vrchslatina – an experimental design and the main aims. *Lesnícky časopis - Forestry Journal* 59:203–213.
- Kozłowski, T. T., 1964: Shoot growth in woody plants. *Botanical Review* 30:335–392.
- Kozłowski, T. T., Pallardy, S. G., 1997: *Physiology of Woody Plants*. San Diego, Academic Press, 411 p.
- Kunstler, G., Curt, T., Bouchaud, M., Lepart, J., 2005: Growth, mortality, and morphological response of European beech and down oak along a light gradient in sub-Mediterranean forest. *Canadian Journal of Forest Research* 35:1657–1668.
- Lindholm, M., Ogurtsov, M., Aalto, T., Jalkanen, R., Salminen, H., 2009: A summer temperature proxy from height increment of Scots pine since 1561 at the northern timberline in Fennoscandia. *Holocene* 19:1131–1138.
- Lindholm, M., Jalkanen, R., Salminen, H., Aalto, T., Ogurtsov, M., 2011: The height-increment record of summer temperature extended over the last millennium in fennoscandia. *Holocene* 21:319–326.
- Lukac, M., Godbold 2011: *Soil ecology in northern forests: a below-ground view of a changing world*. Cambridge University Press, Cambridge, 268 p.
- Pajčík, J., Konôpka, B., Lukac, M., 2011: Individual biomass factors for beech, oak and pine in Slovakia: a comparative study in young naturally regenerated stands. *Trees* 25:277–288.
- Priwitzer, T., Capuliak, J., Bošela, M., Schwarz, M., 2013: Preliminary results of soil respiration in beech, spruce and grassy stands. *Lesnícky časopis - Forestry Journal* 59:189–196.
- Rewald, B., Leuschner, Ch., 2009: Belowground competition in a broad-leaved temperate mixed forest: Pattern analysis and experiments in a four-species stand. *European Journal of Forest Research* 128:387–398.

- Reynolds, E.P., Frochot, H., 2003: Photosynthetic acclimation of beech seedlings to full sunlight following a major windstorm event in France. *Annals of Forest Science* 60:701–709.
- Saliminen, H., Jalkanen, R., 2004: Does current temperature contribute to the final shoot length on *Pinus sylvestris*? A case study at the northern conifer timberline. *Dendrochronologia* 21:79–84.
- Saliminen, H., Jalkanen, R., 2005: Modelling the effect of temperature on height increment of Scots pine at high latitudes. *Silva Fennica* 39:497–508.
- Schmidt-Vogt, H., 1977: *Die Fichte (Band I) – Taxonomie, Verbreitung, Morphologie, Ökologie, Waldgesellschaften* Parey, Hamburg, 647 p.
- Šamonil, P., Vrška T., 2008: Long term vegetation dynamics in the Šumava Mts. Natural spruce-fir-beech forests. *Plant Ecology* 196:197–214.
- Šebeň, V., Bošela, M., Konôpka, B., Pajčík, J., 2013: Indices of tree competition in dense spruces stand originated from natural regeneration. *Lesnícky časopis - Forestry Journal* 59:172–179.
- Tognetti, R., Johnson, J.D., Michelozzi, M., 1997: Ecophysiological responses of *Fagus sylvatica* seedlings to changing light conditions. I. Interactions between photosynthetic acclimation and photoinhibition during simulated canopy gap formation. *Physiology of Plants* 101:115–123.
- Wang, Y., Čufar, K., Ekstain, D., Liang., E., 2012: Variation of maximum tree height and annual shoot growth of Smith fir at various elevations in the Sygera mountains, southern Tibetan Plateau. *PLoS ONE* 7:1–9.