



INDICES OF TREE COMPETITION IN DENSE SPRUCES STAND ORIGINATED FROM NATURAL REGENERATION

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This paper aims to quantify relationships between the biometric parameters of young, 15-year old spruce stands at the Experimental Site Vrchslatina. In 2011, 40 spruce trees were selected to cover four classes of bio-sociological status (dominant, co-dominant, sub-dominant, and suppressed – 10 individuals each). The trees were measured for their height increments (by recording the distances between the successive whorls) and the increments of lateral branches at all whorls. The sample trees were then cut down and discs were taken from the stem base. In the laboratory, the discs were measured for the annual ring widths using WinDendro software. We focused on detailed analyses of the relationship between the bio-sociological status of the trees on the radial and height increments. Minor differences were found in the increments in the newest lateral whorls. The ratio between height increments and lateral branch increments was found to be higher in dominant trees (height increments is two times higher than the increments on the lateral branches). Conversely, the smallest ratio was found in suppressed trees (the ratio was around 1). The ratio between tree height and diameter at the stem base, as well as the ratio between height and radial increments, was the smallest for dominant and the highest for suppressed trees. Hence, relationships between height and diameter increments (both annual and cumulative) proved to reflect competition intensity among trees.

Keywords: *young spruce trees, natural regeneration, inter-tree competition, height increment, diameter increment*

1. Introduction

Competition has been identified as the main factor influencing the mortality of trees in forests in the temperate zone (EID & TUHUS, 2001; YANG *et al.*, 2003; MONSERUD *et al.*, 2004). The fastest competitive dynamics take place in the youngest and densest stands, where numbers of individuals may reach millions of trees per hectare. Here, competition is primarily driven by the density of vegetation. It affects the stability, but also the productivity of stands. Neighboring individuals interact with each other in the canopy, but – sometimes more importantly – belowground. Some of the most visible consequences of competition are the shape and the dimensions of the stem. Other significant features affected by competition are the degree of tree taper and presence of knots, which determine the technical and

economic utilization of timber logs. Mutual competition of tree crowns also changes the size of leaf area and morphological characteristics of leaves (BARNÁ, 2004). Any competition between plants modifies the ratio of photosynthetic apparatus biomass (i.e. assimilation organs) to the total tree biomass. Moreover, KONÓPKA *et al.* (2010) showed contrasting values for woody compartments' production on a foliage biomass unit (growth efficiency) between tree individuals grown in different forest vertical layers (dominant or suppressed trees), as well as between stands at different growth stages and of different densities. These findings suggest that competition not only modifies the structure of the biomass, but also changes physiological processes and carbon fluxes in forest ecosystems. Furthermore, it can be assumed that the competition affects wood production, wood

quality and resistance of trees to destructive factors or injurious agents (in particular resistance to wind and snow destruction).

Competition relationships can be intra-specific (within one tree species such as in spruce monocultures or homogeneous beech forests) or inter-specific (multiple combinations of several tree species). Regeneration, growth and development of plants in the juvenile growth stages are also affected by the competition from other vegetation (ground vegetation). The conditions for regeneration under mature trees differ significantly from those growing on a clear cut area. While beech and spruce regeneration growing under the parent forest stand is often limited by light availability and driven by the size of the gaps (JARČUŠKA & BARNA, 2011; ŠAMONIL & VRŠKA, 2008), juvenile individuals growing on clear-cut areas are usually under severe pressure from competing vegetation.

The main factor driving aboveground competition is light availability, whereas belowground we can usually identify several factors which play a part in determining plant growth (e.g. moisture and soil temperature, amount of nutrients). A common feature of the rhizosphere in forest gaps and clear-cut areas is – as in the case for the above-ground part - an abundance of uncolonised space (WILCZYŃSKI & PICKETT, 1993). Competitive relationships between trees are critical to almost all aspects of forest ecology and their understanding is crucial for the management of forest ecosystems (THORPE *et al.*, 2010). This knowledge is also crucial for the development of sustainable management options in forest ecosystems, especially those featuring mixed species or uneven-aged structures (CANHAM *et al.*, 2006). Competition relationships in managed forests are guided by long-term silviculture and conservation strategies, which aim at ensuring static stability and/or increased production. The ultimate aim of the managed growth process is a regular annual volume increment; however competition affects its distribution and quantity.

Currently, several studies have been undertaken to research the competition relationships in forests. The most relevant are probably the results from permanent research plots which focused on forest production and the effects of thinning. Despite the potential of such studies, we still lack information about competition relationships in mixed stands, biomass allocation at young stages, growth efficiency, quantity, quality and distribution of assimilation organs or fine roots. Great opportunities for important contributions still loom in the research of light conditions and dendrochronological analyses.

Since height and diameter increments of trees do not follow the same course (growth intensity) throughout the entire tree life (OLIVER & LARSON, 1996), a temporal change to the height to diameter ratio (HD ratio) occurs. In general, to predict development of the HD ratio over time, either stand age or size (mean height or diameter)

can be used. Mountain spruce forests in Slovakia (at very high altitudes), KONÔPKA & KONÔPKA (2003) showed decreasing values of the HD ratio with increasing mean stand diameters. The course of temporal development of the HD ratio as well as its value at a particular point in time is most likely related to two groups of factors: forest stand characteristics and properties of the abiotic environment around the stand. Among forest stand characteristics, stand density (or size of gaps between trees) has been recognised as important (e.g. OPIO *et al.*, 2000; NILSSON, 1993). Spacing trials and experiments on different intensities of thinning in coniferous stands have clearly demonstrated the value of the HD ratio increases with the number of tree per unit area (MÄKINEN *et al.*, 2002, HARRINGTON *et al.*, 2009). WANG *et al.* (1998) demonstrated that increasing tree size (bio sociological position) in a stand decreased the value of the HD ratio. Thus, a significant effect on growing space and light availability on the ratio can be assumed.

The aim of the paper was to compare relationships (ratios) between tree height, diameter and upper branch increments among young spruces of specific bio-sociological status. The tested hypothesis was that various sociological statuses of trees modify relations between height and diameter increments. We were interested not only in the ratios for individuals by classes of bio-sociological status in the current year but also, retrospectively, for the trees' entire lives. The ratios between tree height, diameter and branch increments were considered as indicators of competition stress among trees.

2. Material and Methods

Experimental plots established in the Experimental Site Vrchslatina were used for the study. Detailed descriptions of the experimental site are presented in KONÔPKA *et al.* (2013).

2.1. Biometric measurements

One of the experiments at the Experimental Site was aimed at modelling growth dynamics of spruce trees. The dataset used for this paper included 40 young spruce trees originating from natural regeneration after a clear-cut in 1994 – 1996. In 2011, the age of the trees ranged from 11 to 17 years. Trees were cut down at the end of the growing season for the year 2011 and taken to the laboratory. The samples were selected to represent four categories of tree bio-sociological status in the nearly even-aged forest stand: dominant trees (I), co-dominant (II), sub-dominant (III), and suppressed (IV). Thus, 10 trees were selected for the each category. The samples were measured for their biometric characteristics such as tree height (with a precision of 1 cm), diameter at the tree base (DAB) in two perpendicular measurements (with a precision of 1 mm), and diameter at breast-height (DBH) in two perpendicular measurements (with a precision of 1 mm). The samples were cut at the stem base and height

Table 1. Basic statistical characteristics of analysed trees

Bio-sociological status	Diameter at base (DAB) over bark	Diameter at base (DAB) inside bark	Diameter at breast height (DBH)	Height (H)	Ratio DAB/DBH	Ratio H/DBH
	[mm]			[m]	[m/m]	
I. Dominant	109 ± 24	95 ± 24	73 ± 13	6.1 ± 0.6	1.49 ± 0.11	85.7 ± 9.7
II. Co-dominant	56 ± 8	45 ± 8	39 ± 7	4.1 ± 0.4	1.43 ± 0.12	104.3 ± 10.9
III. Sub-dominant	31 ± 6	26 ± 5	20 ± 5	2.8 ± 0.5	1.58 ± 0.23	148 ± 22.6
IV. Suppressed	22 ± 4	18 ± 3	11 ± 3	1.9 ± 0.3	2.16 ± 0.54	191.2 ± 38.5

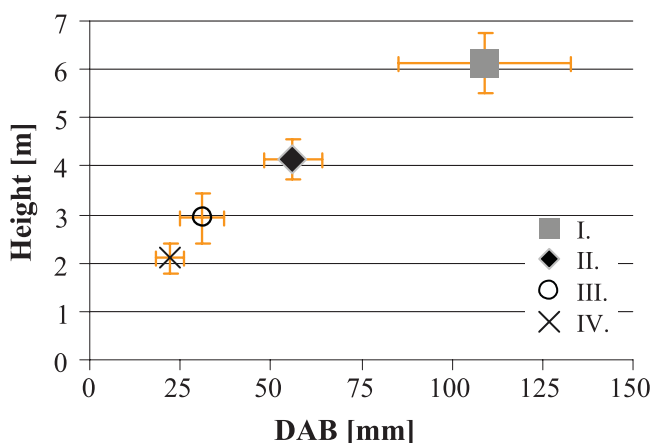


Fig. 1. Height and diameter structure of analysed trees by bio-sociological classes (average ± SD)

increments were measured backwards from the latest to the earliest (the very first height increments that were recognizable) with the precision of 1 cm. The ability to recognize the whorl to measure the height increments decreased towards stem base. At the same time, lateral twig increments were measured. In every whorl the numbers of branches were counted and an average-sized branch was visually identified and selected for each whorl. Twig increments (lengths) towards the rear of the tree trunks were measured in every selected branch. Twig increments with and without needles were also recognized.

Basic statistics of the samples are presented in Figure 1 and in Table 1. DBH measured in the field is presented as the diameter outside bark (further analyses using the sampled cross-section used the diameter inside bark).

2.2. Laboratory analyses

Tree-ring widths (TRW) were measured for the cross-sectional samples in the laboratory. The samples were air-dried and sanded to ensure the annual rings were clearly visible. The samples were scanned using the required resolution and the TRWs were measured using WinDendro (Regent Instruments). The TRWs were measured at four directions perpendicular to each other. The clarity of the annual ring decreased towards

the stem pith, which may have affected the accuracy of the TRWs at the younger stages. Cross-dating was performed through the comparison of measurements from the four directions. In addition, the height increments were used to help cross-dating.

2.3. Data processing

Standard statistical methods were used for data processing and analyses were performed in MS Excel and Statistica (StatSoft Inc., 2011). We calculated tree characteristics such as diameter, height, increments of lateral twigs, and ratios between them within every bio-sociological status of trees (I–IV). Means and standard deviations were calculated from all trees. However, the age variability meant that mean was not always calculated from the same number of trees (max. 10 for every bio-sociological status, particularly for the first analysed years was a lower number), which may have had an impact on the representativeness.

3. Results and discussion

Height and diameter increments of spruce trees since 1994 were analyzed (Table 2). However, only the last 13 years (since 1998) were further selected for the study due to sample size requirements (8 trees from the total 10 trees). In addition, the period 2000 – 2011 was used for analysis of the increments of the lateral branches. Results suggested that the spruce natural regeneration was established in 1996. The average value of age in the spruce stand was 15 years in 2011.

Before analysis, trees were clustered into the four categories of bio-sociological status and basic statistics for the clusters are listed in Table 1 and Figure 1. Dominant trees were found to have 2-times higher DAB and DBH compared to co-dominant trees. The difference increased to 3-fold compared to sub-dominant and 4-fold compared to suppressed trees (concerning tree height the ratio is: 100:66:46:33).

Differences of height-diameter ratio (HD) of young trees between bio-sociological statuses were also high. Dominant trees had a ratio below 90, with the highest static stability. The more suppressed the trees, the higher the HD ratio and lower the static stability.

Table 2. Basic characteristics of increment in 2011

Bio-sociological Status	Height increment ΔH	Diameter increment ΔDAB	Lateral increment ΔL	Ratio $\Delta H / \Delta DAB$	Ratio $\Delta L / \Delta H$
	[m]	[mm]	[m]	[m/m]	[m/m]
I. Dominant	0.88 ± 0.12	16.7 ± 5.3	0.45 ± 0.06	55.6 ± 11.1	0.51 ± 0.11
II. Co-dominant	0.64 ± 0.12	7.0 ± 3.2	0.36 ± 0.07	117.4 ± 70.3	0.56 ± 0.11
III. Sub-dominant	0.25 ± 0.18	2.0 ± 0.8	0.17 ± 0.09	121.7 ± 71.8	1.12 ± 0.78
IV. Suppressed	0.11 ± 0.11	1.0 ± 0.8	0.1 ± 0.05	137.6 ± 143.4	1.25 ± 0.46

3.1. Increments in year 2011

Mean height, lateral and diameter increments for each bio-sociological status are presented in Table 2.

When the trees were 15-years old, dominant trees had 8-times higher height increments than suppressed, 4-times than sub-dominant, and 1.4-times than co-dominant. Even greater differences were found for diameter increments. Dominant trees had 16-times higher diameter increments than suppressed trees, 8-times higher than sub-dominant, and 2-times higher than co-dominant. Contrary, smaller differences were found for the increments of lateral branches (dominant trees had 4-times higher than suppressed). Dominant trees had 50-times higher diameter than height increments, co-dominant trees had 100-times, and suppressed even 130-times higher.

The same results were found for lateral-to-height increments. Dominant and co-dominant trees had 2-times higher height increments than lateral, but sub-dominant and suppressed trees had diameter growths more intensive than height growth. It is assumed that this was due to high inter-tree competition and the shading effect of the suppressed trees which causes a higher suppression of height increments than lateral ones.

3.2. Height growth

Height increments of spruce are generally lower for lower bio-sociological status' (it decreases from dominant to suppressed trees) (Figure 2).

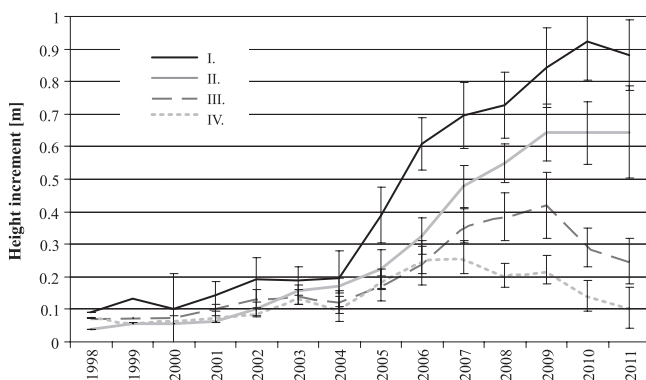


Fig. 2. Development of average height increments according to bio-sociological status (whiskers denote standard deviation)

Also, height increments decreased during the last 3 years for sub-dominant and suppressed trees probably due to the higher shading effect (Figure 2). Until 2004, the differences of height increments were found to be insignificant. It is supposed that trees reached similar bio-sociological status until 2004. Here we would like to point out large differentiation of height increments among spruces in the stand since 2005. Perhaps some trees reached dominant status and their size (volume of crown) limited light resources for the other individuals. Hence, we might assume considerable aboveground competition press in the stand since the aforementioned year. Obviously, a similar situation would occur also in the rhizosphere (root competition) at some stage of the stand development. However, this matter was not part of our research interest.

3.3. DAB growth

Similar to height growth, trees had different DAB growth at different bio-sociological status (Figure 4, 5).

Dominant trees had increments 2-times higher than co-dominant since 2003 and co-dominant trees' growth rate was 2-times higher than sub-dominant and suppressed trees. No essential differences were found between the sub-dominant and suppressed trees but the sub-dominant trees tend to have higher diameter growth.

Contrary to height increments, trees were found to decrease their DAB increments in 2009, which was

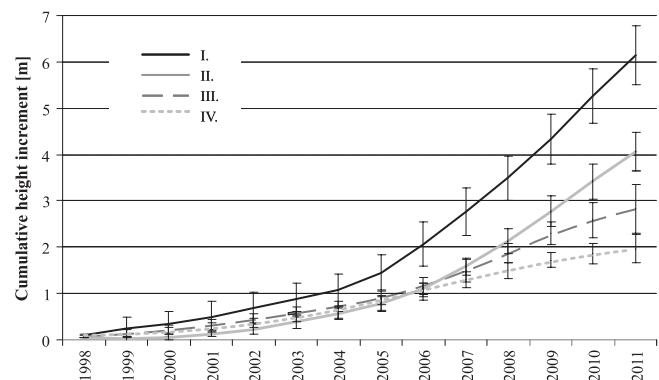


Fig. 3. Height grow development according to bio-sociological status (whiskers denotes standard deviation)

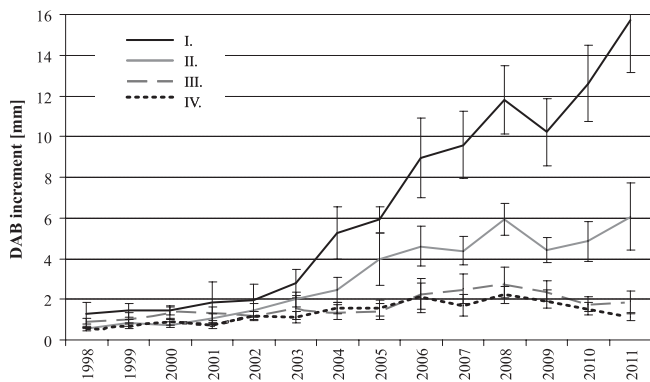


Fig. 4. Development of DAB increments according to bio-sociological status (whiskers denote standard deviation)

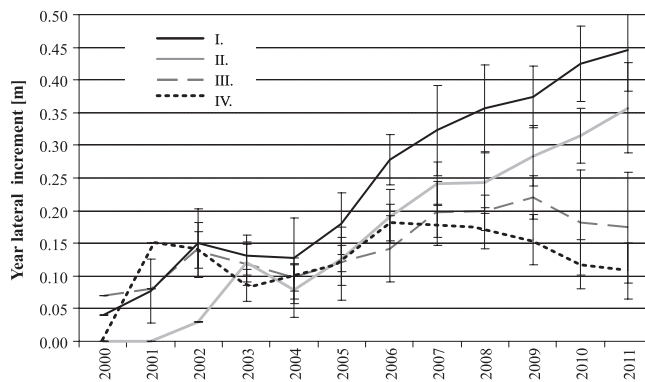


Fig. 6. Development of average lateral increments according to bio-sociological status (whiskers denotes standard deviation)

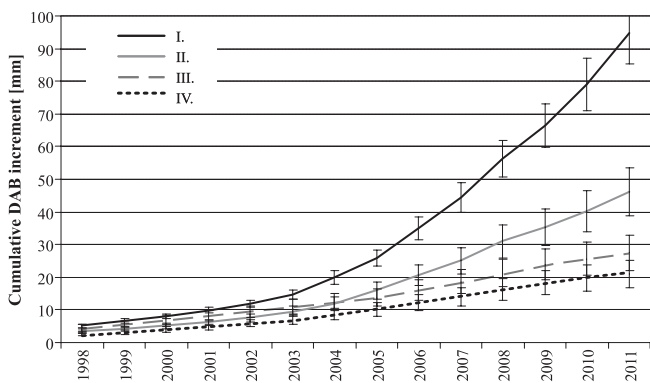


Fig. 5. Development of cumulative DAB increments according to bio-sociological status (whiskers denote standard deviation)

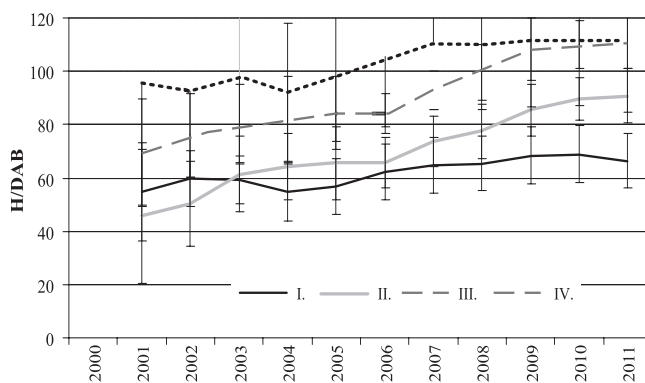


Fig. 7. Development of H/DAB ratio (whiskers denotes standard deviation)

probably caused by harsh weather conditions during that year (especially drought at the beginning of the growing season).

As we have commented, differentiation for height increments at certain stages of the development of the stand, similar phenomenon was also recorded for diameter increments. However, a clear diameter increment differentiation occurred previously in 2004, i.e. one year earlier than for height increments. This finding suggests that worsening light conditions influence earlier stem thickening than terminal elongation.

3.4. Lateral growth of branches on upper whorl

Branches of selected spruce trees had their lateral increments, since 2000, similar to height and diameter increments. The lateral increments were significantly different between trees in different bio-sociological statuses (Figure 6). Similarly, a decrease of the increments was found during the last 3 years for sub-dominant and suppressed trees.

3.5. Ratios between height, lateral and DAB increments

Height-diameter ratio (H/DAB) is an index which may, similar to slenderness quotient, be used as an indicator of the static stability of trees.

Long-term increases of the H/DAB can be seen in Figure 7. The lowest trend was found for dominant trees with the mean ratio of 60. Co-dominant trees reached H/DAB ratio 50–60 in 2001 (when they were 5 years of age), and since then it increased to 90 in 2011. A similar trend was found for sub-dominant trees, but the mean H/DAB ratio was lower (70–110) during whole study period. The highest ratio was found for suppressed trees (90–110).

The ratio between height (increments of the lateral branch in the first whorl starting from the tree top) and diameter increments had similar trends like H/DAB ratio (Figure 8). However, the differences between the categories of bio-sociological status were not as high as the previous ratio; mean ratios even crossed each other in some years.

The ratio increased for co-dominant trees from 80 to 120. An increase was also found for sub-dominant and suppressed trees.

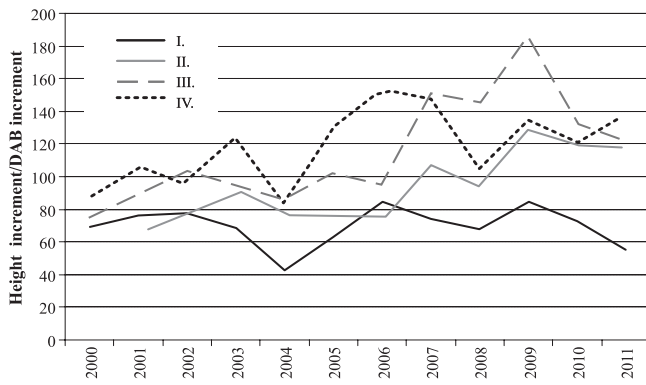


Fig. 8. Development of ratio height increments/DAB increments

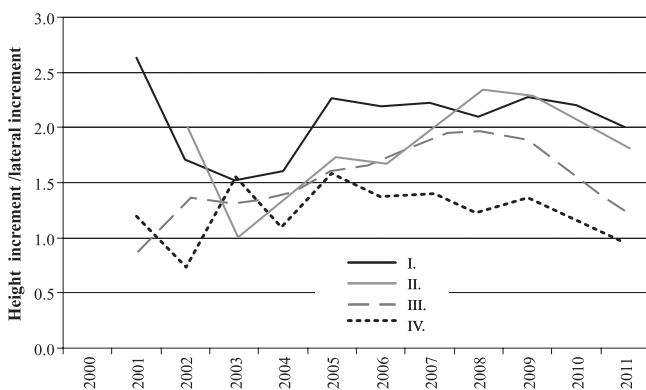


Fig. 9. Development of ratio height increments/lateral length increments

Opposite sequences of bio-sociological statuses was found for the ratio between height and lateral increments (Figure 9). The highest ratio was found for dominant trees. On the contrary, suppressed trees had stable ratios during the whole study period. It means that the height increments of young dominant trees were 2-times faster than lateral increments, but both increments were similar for suppressed trees. However, huge variability was found between trees.

Figure 10 presents the height growth of trees in different bio-sociological status. The height growth is obviously different between trees from different status. The highest growth rates were found for suppressed and sub-dominant trees, but the lowest for dominant trees.

In combination with height development (Figure 3) it is possible to determine that the age dominant trees needed to reach 2 m in height is 10 years. It took 2 more years for co-dominant trees to reach 2 m in height, 3-years for sub-dominant, and 5-years for suppressed trees. Dominant trees reached a height over 6m when they were 15 years old.

However, the problem with comparing the growth rate of different categories of bio-sociological status is that

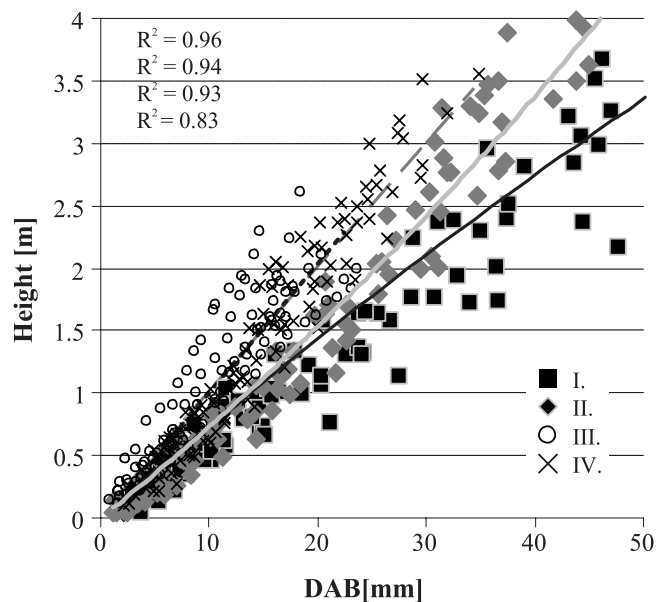


Fig. 10. The relationship between DAB and height according to bio-sociological status of spruce trees (all measurements together)

this status was determined during the last measurement in 2011. It is possible that individual trees had changed their status during the observation period. These possible changes were not detectable since trees were selected individually and they do not create one bio-group or forest stand. The results showed that dominant trees kept their status for a long time and the highest differentiation probably occurred in sub-dominant and suppressed trees. It is likely that in the beginning when the trees were not growing in close-canopy, the trees were growing in the same bio-sociological status.

To summarize our results, we can state that large differences in height-diameter ratio between the trees in the specific bio-sociological position (eventually of contrasting sizes) in the observed young stands. This finding is in accordance with papers from a variety of authors but those were prevalently interested in older stages of growth. This relationship was proved for instance in spruce stands (WIKLUND *et al.*, 1995) but also in stands of many other coniferous and broadleaved species (WANG *et al.*, 1998). On the other hand, we assume that our results are original especially in terms of the description of height-diameter ratio course during more than one decade. Moreover, we did not find any paper showing the relationship between height increments and upper branch elongation with regard to bio-sociological position of trees. This kind of study may contribute to a better understanding of growth strategies (carbohydrate allocate into the above-ground compartments) of trees under contrasting competition stress.

4. Conclusions

The most intensive growth changes can be found in young growth stages, and inter-tree competition pressure can be considered as having a major effect. The inter-tree and inter-species competition in young growth stages are not well known compared to further, older growth stages and it has potential for more intensive research.

The results from young and dense spruce stands show large differences in growth rates between trees from different bio-sociological status. The most evident differences were found for height and diameter increments, less for lateral increments (at the branches from the upper whorl of a tree). However, the ratio between height and lateral increments seems to be a good indicator of inter-tree competition. While in the dominant trees, the ratio reached the value 0.5 (meaning that the lateral increments is half the height increments), for suppressed trees it had values between 1 and 2. On the other hand, high variability of the value was found for suppressed trees. Large inter-tree competition may have, however, caused shifts of trees between bio-sociological statuses and it then influenced determining the tree status back to an earlier time.

In addition, the results showed that dominant trees were, at the same height, larger in diameter at stem base than co-dominant, and co-dominant larger than sub-dominant and suppressed trees. Suppressed trees were not higher than 2 m, while some dominant trees reached over 6 m of height.

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Resumé

Kompetícia a kompetičné vzťahy predstavujú v lesoch mierneho pásma hlavný faktor vplývajúci na mortalitu stromov. Najväčšia dynamika prebieha v najmladších rastových stupňoch, ktoré sú najpočetnejšie, pričom tu počty jedincov dosahujú až milióny kusov na hektár. Kompetícia závisí v prvom rade od hustoty porastu. Vplyva na stabilitu ale aj na samotnú produkciu porastov. Susedné jedince sa navzájom ovplyvňujú v korunovom priestore, ale takisto v koreňovom systéme pod povrchom zeme. Následky kompetície sa prejavujú aj na tvare kmeňa a jeho vlastnostiach. Významný je napríklad vplyv na zbiehavosť kmeňa či hrčatosť, čo determinuje technické a ekonomické využitie dendromasy. Kompetičné tlaky medzi drevinami modifikujú podiel biomasy fotosyntetizujúcej časti stromov (t. j. asimilačných orgánov) k celkovej stromovej biomase. Tento podiel sa vo fyziológii nazýva rastová efektívnosť (growth efficiency) a predošlé výskumy (napr. KONÓPKA *et al.*, 2010) naznačili veľké rozdiely medzi jedincami rôzneho biosociologického postavenia, ako aj medzi porastmi rôzneho vývojového štádia a rôznej hustoty.

Cieľom príspevku bolo porovnať vzťahy medzi výškou stromov, hrúbkou pri koreňovom krčku a prírastkoch na bočných vetvách mladých smrekov v rôznom sociologickom postavení. Hypotéza bola, že rôzne biosociologické postavenie spôsobuje modifikáciu vzťahov medzi výškovými a hrúbkovými prírastkami. Použili sa pokusné plochy Výskumného objektu (VO) Vrchslatina, na ktorom je založených mnoho experimentov. Podrobný popis VO je prezentovaný v práci KONÓPKA *et al.* (2013).

Retrospektívnou analýzou sa zistili výškové i hrúbkové prírastky, pri najstarších stromoch až do roku 1994 (17 rokov späť). Pri vyhodnocovaní bočných prírastkov na vetvách bol východiskový až rok 2000 (iba 11 rokov späť). Na základe analýz sme zistili najstaršie prírastky medzi rokmi 1994 až 1998, pričom za rok vzniku porastu sme stanovili rok 1996. Teda v roku 2011 mali analyzované jedince vek priemerne 15 rokov.

Priemerné rozmery analyzovaných vzorníkov tvorili 4 výrazne oddelené kategórie. Nadúrovňové jedince vykazujú priemerne asi dvojnásobné hrúbky d_0 ale i $d_{1,3}$ oproti úrovňovým, viac ako 3-násobné oproti vrastavým a viac ako 4-násobné oproti podúrovňovým smrekom (pri výškach je pomer asi 100 : 66 : 46 : 33). Štíhlostný kvocient ($h/d_{1,3}$ ratio) mladých smrekov je výrazne rozdielny. Nadúrovňové jedince vykazujú hodnoty vysokej statickej stability s hodnotami pod 90, s poklesom sociologického postavenia nastáva vzostup do menej staticky stabilných hodnôt.

Z meraní vyplynuli zistenia o vyššej, ale v určitých prípadoch aj nižšej tesnosti korelácie medzi posudzovanými veličinami. Preukázal

sa výrazný vplyv biosociologického postavenia smrekov na výškové a hrúbkové prírastky, menej výrazné diferencie boli pri porovnaní priemerných dĺžok bočných vetiev na hornom praslene. Kým pri kompetične silných nadúrovňových a úrovňových smrekoch v mladine dosahuje pomer medzi bočným a výškovým prírastkom na vetvách a terminálnom výhonku najčastejšie hodnotu približne 0,5 (teda rast do šírky je polovičný oproti rastu terminálu), pri kompetične potláčaných vrastavých a podúrovňových smrekoch v mladine dosahuje opačný pomer s hodnotami najčastejšie medzi 1 – 2. Na druhej strane sa tu zistila oveľa väčšia variabilita ako pri úrovňových smrečkoch. Zistilo sa, že nadúrovňové jedince sú pri rovnakej výške hrubšie ako jedince úrovňové, tie zas hrubšie ako jedince vrastavé a podúrovňové. Rovnako sa zistilo, že na dorastenie do rovnakej výšky potrebujú najkratší čas nadúrovňové jedince, dlhší úrovňové, najdlhší vrastavé a podúrovňové jedince. Tie v danom výskumnom objekte neprekročili výšku 2 m, keď nadúrovňové presiahli priemerne 6 m a úrovňové 4 m.