
The paper analyses the height structure of mountain spruce forests in the nature reserve Babia hora, Slovakia. The analysis consisted of the three partial tasks (1) analysis of the relationship between maximum tree height and elevation, (2) derivation and evaluation of height-diameter curves separately for species and elevation categories, (3) frequency analysis of tree heights. The results revealed a tight correlation of maximum tree height to elevation (correlation index equal to 0.91), and between tree height and diameter (correlation index varied from 0.93 to 0.99). For Norway spruce (Picea abies L./Karst), height-diameter relationship was described by a five-parameter exponential function, because simpler functions were not able to represent the small values below the usual truncation point satisfactorily. In case of rowan (Sorbus aucuparia L.), Gompertz function was used for the description of height-diameter relationship. Tree height frequencies were analysed by frequency analysis. The results indicated that the most differentiated vertical structure is in the stage of growth. The stage of breakdown is characterised by bimodal distribution. With increasing elevation the differences between the vertical structure of the stage of optimum and breakdown diminish, while the differences between the stage of growth and the stages of optimum and breakdown become more distinct.

Keywords: Height-diameter curve, height frequency, elevation, developmental stages, natural forest

Introduction

The structure of a forest can be described by several attributes including horizontal spacing, vertical stratification, size, age and species composition (Svensson, Jeglum 2001). Although the most common approach is to use diameter distribution (O’Hara 1998), vertical stand structure is also an important feature of forest ecosystems, as it reflects key factors, such as site conditions, as well as ecological processes, e.g. competition, or disturbance regimes (Montes et al. 2008). Hence, Svensson, Jeglum (2001) concluded that height distribution may also be a relevant measure of forest structure and ongoing processes within an ecosystem. An overview of the schemes proposed for the description of the structure of mountain spruce forests in Europe and presented by Kucbel et al. (2008) showed that vertical structure had been taken as one of the basic criteria in these classifications. Height differentiation has also been used as a basis for distinguishing developmental stages in natural forests (Korpeľ 1995, Hladík et al. 1993). In general, natural forests are believed to be structurally more heterogeneous than managed forests (Svensson, Jeglum 2001). On the other hand, the research of mountain spruce forests in the
Carpathians showed that these forest stands are predominantly homogeneous composed of a single storey (Korpeľ 1995, Gubka 2004, Kucbel et al. 2008).

Apart from the forest development, forest stand structure is also known to change with elevation (Krušpán 2009). Elevation is a characteristic closely correlated to climate factors that are primary influencing factors determining tree growth. Since elevation is an easy-to-measure characteristic, it is often used as a surrogate variable. Korpeľ (1995), and Merganič et al. (2003) reported that elevation 1,400 m above sea level represents a border line, below which the differences between the developmental stages become more distinct, while above it the differences diminish.

Considering the above-stated facts, the goal of the presented work was to analyse the height structure of the mountain forest stands in the nature reserve Babia hora, Slovakia with regard to the developmental changes and elevation gradient.

Material and methods

The data used come from the region of the Babia hora national nature reserve. The reserve was established in 1926 and enlarged in 1974 to its contemporary size of 503.94 ha (Korpeľ 1995). The mountain massif of Babia hora is a part of the outer Western Carpathian mountain range lying in the northern part of Slovakia at the border to Poland. The forest stands of Babia hora are composed almost entirely of Norway spruce (Picea abies L. Karst.) with a small admixture of silver fir (Abies alba Mill.) and rowan (Sorbus aucuparia L.).

In the area of the Babia hora national nature reserve, 57 permanent circular sample plots were established in 2002 (Merganič et al. 2003), each with an area of 0.05 ha (i.e. radius = 12.62 m). The plots are located at an elevation from 1,100 m above sea level to the timber line (approximately 1,500 m). They are equally distributed to four pre-defined elevation categories (below 1,260 m; 1,260–1,360 m; 1,360–1,460 m and above 1,460 m above sea level) and three developmental stages of virgin forests: stage of growth, optimum and breakdown as defined by Korpeľ (1995). On each sample plot, every tree with a diameter at breast height (dbh) above 7 cm was measured. Trees higher than 1.3 m but with dbh < 7 cm were measured on the second concentric circle. Its radius was estimated directly in the field according to Smelko (1968), who defined the optimum plot size as one that contains 15 to 25 trees. However, the size of this second concentric plot never exceeded the area of the first circle, i.e. its maximum radius was 12.62 m.

All together, 2,846 individuals were measured, out of which 1,738 trees were living trees (1552 individuals of Norway spruce (Picea abies L. Karst.), 178 individuals of rowan (Sorbus aucuparia L.) and 8 individuals of European beach (Fagus Sylvatica L.), 414 standing dead trees, 225 naturally formed stumps, and 469 lying coarse deadwood pieces. In addition, 513 individuals of young trees up to the height of 1.3m were measured.

The analysis of the height structure accounted only for living trees and consisted of the three partial tasks:

- Analysis of maximum height as a function of elevation
- Development of height-diameter curves
- Frequency analysis of tree heights.

The first part of the analysis is aimed at the construction of a simple model that describes the relationship between the maximum height and elevation. Maximum height represents the maximum tree height recorded in the sample plot. From several mathematical functions that were applied to data the following exponential equation was chosen as the one that described the analysed relationship best:

\[ y = \left(1 - e^{a_0 + a_1 x + a_2 x^2 + a_3 x^3 + a_4 x^4}\right) \cdot a_5 \]

where \( y \) is maximum tree height in metres, \( x \) is elevation in metres above sea level, and \( a_0 \) to \( a_5 \) are parameters of the equation.

Height-diameter curves were developed using only the data of undamaged living trees. The height-diameter curve for Norway spruce (Picea abies L./Karst.) was best represented by the function as follows:

\[ y = \left(a_6 - e^{a_7 x + a_8 x^2}\right) \cdot a_4 \]
In case of rowan (Sorbus aucuparia L.), Gompertz function (Šmelko et al. 1992) was used:

\[ y = \frac{a_0}{(a_1)(a_2)^x} \]  

where \( y \) is tree height in metres, \( x \) is tree diameter at breast height in centimetres, and \( a_0 \) to \( a_4 \) are parameters of the equation.

The development of height-diameter curves and the selection of the functions was driven by two requirements: the function should have had to perform logically (if tree diameter is 0 cm, tree height is equal to 1.3 m), and the correlation should have had to be as close as possible (given by the correlation index and the error of the regression curve).

Tree height frequencies were analysed by frequency analysis for all trees together and separately for Norway spruce, while tree heights were divided into 1 m height classes.

**Results**

Maximum recorded height of spruce was 44 m. This tree grew in the first elevation category in the stage of optimum. Maximum recorded height of rowan was equal to 14 m, and it was also recorded in the first elevation category, but in the stage of growth.

**Relationship between elevation and maximum tree height**

The estimated parameters of function [1] describing the relationship between tree height and elevation are given in Table 1. Note that the function is valid only within the elevation range, for which it was parameterised, i.e. from 1,173 to 1,503 m above sea level, and should not be used outside this range without its prior testing.

Maximum tree height significantly decreases with increasing elevation (Fig. 1). As shown in Table 1, the correlation between elevation and maximum stand height is close, as the suggested function explains approximately 82% of the variability of maximum height. The rest, i.e. 18%, is caused by random factors and factors which are not accounted for in our analysis. However, the error of the estimation of maximum height on the base of elevation is quite large, since its absolute value is 3.9 m at 68% confidence level.

**Tab. 1: Parameters of function [1] describing the relationship between the maximum height and elevation, and its statistical description**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a_0 )</td>
<td>-1984.12663</td>
</tr>
<tr>
<td>( a_1 )</td>
<td>5.87253462</td>
</tr>
<tr>
<td>( a_2 )</td>
<td>-6.51265417×10(^{-3})</td>
</tr>
<tr>
<td>( a_3 )</td>
<td>3.20502521×10(^{-6})</td>
</tr>
<tr>
<td>( a_4 )</td>
<td>-5.90286×10(^{-10})</td>
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<tr>
<td>( a_5 )</td>
<td>56.29</td>
</tr>
</tbody>
</table>

| Number of sample plots (n) | 57 |
| Correlation index | 0.91 |
| Index of determination | 0.82 |
| Absolute standard error of function (m) | 3.94 |
| Relative standard error of function (%) | 17.70 |
Fig. 1: Relationship between maximum tree height and elevation described by exponential function [1]
(Index of determination = 0.82)

Legend:
Elevation categories: ◉ below 1,260 m; □ 1,260 – 1,360 m; ★ 1,360 – 1,460 m and ◔ above 1,460 m above sea level

Zones of height-diameter curves: A – below 1,295 m; B – 1,296-1,375 m; C – 1,376-1,445 m;
D – above 1,446 m above sea level

Tab. 2: Parameters of height-diameter curves for Norway spruce (Picea abies L.) and their statistical descriptors

<table>
<thead>
<tr>
<th>Statistics</th>
<th>Zone of height-diameter curves (m above sea level)</th>
<th>below 1,295</th>
<th>1,296 – 1,375</th>
<th>1,376 – 1,445</th>
<th>above 1,446</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameter</td>
<td></td>
<td>a₀</td>
<td>a₁</td>
<td>a₂</td>
<td>a₃</td>
</tr>
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<td></td>
<td></td>
<td>0.44000</td>
<td>0.11111</td>
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<td>-1.64300</td>
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<td>-0.01153</td>
<td>-0.01250</td>
<td>-0.01900</td>
<td>-0.02600</td>
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<td></td>
<td></td>
<td>-0.00038</td>
<td>-0.00032</td>
<td>-0.00100</td>
<td>-0.00300</td>
</tr>
<tr>
<td>Number of trees (n)</td>
<td></td>
<td>210</td>
<td>247</td>
<td>105</td>
<td>178</td>
</tr>
<tr>
<td>Correlation index</td>
<td></td>
<td>0.99</td>
<td>0.97</td>
<td>0.95</td>
<td>0.96</td>
</tr>
<tr>
<td>Index of determination</td>
<td></td>
<td>0.97</td>
<td>0.95</td>
<td>0.89</td>
<td>0.92</td>
</tr>
<tr>
<td>Absolute standard error of function (m)</td>
<td></td>
<td>2.0</td>
<td>1.9</td>
<td>2.2</td>
<td>0.9</td>
</tr>
<tr>
<td>Relative standard error of function (%)</td>
<td></td>
<td>13.3</td>
<td>16.6</td>
<td>16.4</td>
<td>16.8</td>
</tr>
</tbody>
</table>
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Height-diameter curves

For Norway spruce, we derived four height-diameter curves, each for one elevation zone (A – D in Fig. 1). The zones were estimated visually on the base of the performance of function [1] and maximum tree heights (Fig. 1). The ranges of the zones are as follows: A – below 1,295 m; B – 1,296–1,375 m; C – 1,376–1,445 m; D – above 1,446 m above sea level. When we compare these zones with the pre-defined elevation categories used for the stratification of the area of interest, we can see that both categorisations are very similar. Tab. 2 presents the derived parameters of the curves for each zone including their statistical descriptors. For rowan we derived only one height-diameter curve (Tab. 3), because due to the lack of the data it was not possible to perform a more detailed analysis along the elevation gradient.

As presented in Tab. 2, Tab. 3 and Fig. 2, the relationship between tree diameter and height is very tight, since the correlation index varies from 0.93 to 0.99. Index of determination indicates that the given function describes this relationship between 87 and 97%. The error of estimating tree height on the base of diameter using functions [2] and [3] varies between 85 and 217 cm. The lowest absolute variability is in the highest elevation zone, while the highest is in the third elevation zone (i.e. from 1,376 to 1,454 m above sea level). However, if we examine relative errors, we see that the variability does not change with increasing elevation and remains a constant proportion of height. Average variability of tree heights is 15.8%.

As shown in Fig. 3, Norway spruce height-diameter relationship changes with elevation significantly. Increasing elevation results in decreasing tree height at the same diameter at breast height. A tree with diameter at breast height of 40 cm reaches the height of 25 m if grows below 1,260 m above sea level, but only 10 m if situated above 1,460 m above sea level.

In comparison to spruce, the height-diameter curve of rowan (Fig. 4) is steeper at the beginning, and the height growth culminates earlier, by lower tree diameters. In the region of interest, the presence of rowan trees with higher dimensions is scarce, because rowan grows under a high pressure of dominant spruce and is badly damaged by deer.

Frequency analysis of tree heights

The results of the frequency analysis of tree heights are presented in Fig. 5 and 6. From these figures we can notice the basic theorems that are usually applied for the characterisation of the developmental stages of natural forests, while they are more distinct when analysing only spruce (Fig. 6). In the stage of growth, juvenile height classes dominate, although the variation range of heights extends to higher height classes. They are represented by the trees that grew in the middle storey or understory, and after the dominant trees of the upper storey had fallen out, they got space for finishing their growth process. In the stage of growth, the individuals with maximum dimensions are dominant, while the juvenile trees are missing or are present only sparsely. In the stage of breakdown, the largest individuals begin to fall out and we record a higher proportion of regeneration and individuals in lower height classes.

Tab. 3: Parameters of height-diameter curve for rowan (Sorbus aucuparia L.) and its statistical descriptors

<table>
<thead>
<tr>
<th>Statistics</th>
<th>Zone: 1,170 – 1,490 m above sea level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameter</td>
<td></td>
</tr>
<tr>
<td>$a_0$</td>
<td>10.683</td>
</tr>
<tr>
<td>$a_1$</td>
<td>8.445</td>
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<tr>
<td>$a_2$</td>
<td>0.784</td>
</tr>
<tr>
<td>Number of trees (n)</td>
<td>26</td>
</tr>
<tr>
<td>Correlation index</td>
<td>0.93</td>
</tr>
<tr>
<td>Index of determination</td>
<td>0.87</td>
</tr>
<tr>
<td>Absolute standard error of function (m)</td>
<td>1.2</td>
</tr>
<tr>
<td>Relative standard error of function (%)</td>
<td>15.2</td>
</tr>
</tbody>
</table>
A) Zone below 1,295 m ($R^2=0.97$)

B) Zone 1,296 – 1,375 m ($R^2=0.95$)

C) Zone 1,376 – 1,445 m ($R^2=0.89$)

D) Zone above 1,446 m ($R^2=0.92$)

Fig. 2: Performance of height-diameter curves in individual elevation zones of height-diameter curves for Norway spruce

Legend: ● Growth; □ Optimum; ▲ Breakdown, $R^2$ – Index of determination
Fig. 3: Performance of height-diameter curves of Norway spruce in individual zones of height-diameter curves

Fig. 4: Height-diameter curve for rowan (Sorbus aucuparia L.), Index of determination = 0.87
Fig. 5: Frequency analysis of tree heights in individual elevation categories regardless of tree species.

Legend:
- Growth
- Optimum
- Breakdown

A) Elevation below 1,260 m
B) Elevation 1,260 – 1,360 m
C) Elevation 1,360 – 1,460 m
D) Elevation above 1,460 m

Relative frequency (%)
Height structure of spruce mountain forests of Babia hora – Oravské Beskydy

Fig. 6: Frequency analysis of tree heights in individual elevation categories for spruce
Legend:
- Growth
- Optimum
- Breakdown

A) Elevation below 1,260 m
B) Elevation 1,260 – 1,360 m
Discussion

Tree height significantly reacts to environmental conditions. Therefore, it is one of popular variables used in dendrocentric approach of site index description (Skovsgaard and Vanclay 2008). We detected a significant effect of climate-site gradient expressed on the basis of elevation in the area of interest, when we recorded that in the elevation range of 330 m the height growth potential of Norway spruce (Picea abies L.) decreased from approximately 35 m to 10 m (Fig. 3). Similar findings were presented by Holeksa et al. (2007), who found an average decrease of maximum height by 6 m for each 100 m increment of elevation. The decrease of maximum tree height with increasing elevation was also detected by other authors, e.g. Šrůtek, Lepš (1994), Šrůtek et al. (2002), Svoboda (2005). Due to this, tree height is often used to specify the timberline, although the absolute values defining the treeline range from 1 to 8 metres (Holtmeier 2003).

Tree height has been proven to be a good site index (Fig. 1), which can be used for the stratification of the area into more homogeneous zones. The stratification is important for the mathematical analysis because it reduces the variation of tree and stand characteristics, and accounts for the climate and site gradient that affects the changes in these characteristics. In our case, we pre-stratified the area of interest into four elevation categories (below 1260, 1260–1360, 1360–1460, and above 1,460m above sea level). These elevation categories considerably differ one from another over their diversity (Merganič et al. 2003). As indicated in Fig. 1, the zonation based on maximum tree height corresponds well with the pre-defined elevation categories, as the elevation categories and the zones of height-diameter curves specified for spruce are characterised by a similar maximum tree height in the sample plots.

Height-diameter curves of Norway spruce were described by the five-parameter exponential function because the belt of complete data was not logically and statistically well described by simpler and in forestry more often used height-diameter functions listed in e.g. Šmelko (2000). The shortage of these functions was particularly evident at the beginning of height-diameter curves, since in our case tree heights were measured for all trees, i.e. also in the part which is usually truncated up to a specific diameter at breast height (e.g. 7 cm) in forestry surveys. As stated by Fallah (2009), the quality of height-diameter model is important from several perspectives, e.g. for the estimation of wood volume and increment, for site index determination, or for the explanation of natural succession processes and human-induced changes.

For rowan, it was not possible to analyse the influence of the climatic gradient on the height growth thoroughly due to the lack of data. In the region of interest, vital rowan occurs in the stage of breakdown, is able to occupy space very well and grows faster than spruce as evidenced by the steepness of its height curve (Fig. 4). However, due to the ecological factors, competition of spruce, and game damage, rowan does not achieve the growth potential of spruce. Hence, rowan trees only seldom occur in higher stories. This is evident in the stage of growth, when rowan loses its favourable position. Although the tree height of rowan decreased with increasing elevation, in the fourth elevation category we revealed the reversal. On the base of this fact we assume that at lower elevations the growth of rowan is limited by spruce. At the upper timberline, spruce competition subsides because the forests stands are usually released, and hence, they have sufficiency of light, which in turn results in suitable growing conditions for rowan. In this zone, rowan trees are established under the spruce protection, and can grow at the edge of the groups undisturbed with the culmination of the growth in the stage of optimum and breakdown.

We already stated that increasing elevation has a significant effect on tree height, but it does not influence the variability of heights around the height curve. The values of variation coefficients of the derived height curves for spruce (Tab. 2) are greater than the values reported by Halaj (1978), or they correspond to a higher degree of height differentiation. In the conditions of Babia hora, an average value for spruce is 15.8%. On the contrary, the value for rowan (Tab. 3) conform the findings of Halaj (1978).

The analysis of the frequency curves of tree heights revealed that the most differentiated vertical structure is characteristic for the stage of growth (Fig. 5 and 6). The distribution has a shape of a decreasing curve or a left-skewed asymmetrical curve. As Greig-Smith (1964) stated, reverse-J shaped curves, i.e. negative exponentials, are typical size distributions of individuals in natural forest forms. This curve shape is also typical for selection forests. However, the structure analysis of mountain spruce forests in the Alps and the Carpathians revealed that a differentiated structure of a typical selection forest is either not formed at all, or occurs only in a short period in the stage of growth, and hence is regarded a temporal status (Korpeľ 1995).
The stage of breakdown is characterised by a
bimodal curve, particularly in the first and the
second elevation category (Fig. 5), where the
presence of rowan has a significant positive im-
 pact on the heterogeneity of vertical structure.
In the region of Babia hora, the first and the
second elevation categories are characterised by
the admixture of rowan, which also affects stand
height structure. This is evident in the variation
range, or in the variability of tree heights. If we
analyse only the heights of spruce trees, the co-
efficient of variation decreases by one third from
the overall variability of tree heights regardless
of tree species. On the contrary, in the third
and the fourth elevation category no signifi-
cant changes in variability were found after the
exclusion of rowan trees from the analysis, be-
cause in these elevation categories forest stands
are almost entirely composed of spruce. Based
on these facts we can state that the presence of
rowan significantly increases the variability of
forest stand structure.

With increasing elevation the differences
between the vertical structure of the stage of
optimum and breakdown diminish, while the
differences between the stage of growth and
the stages of optimum and breakdown become
more distinct. If we compare the results of our
analysis with Uemura et al. (1997), we can state
that in the highest 4th elevation category the for-
est structure resembles the typical structure of
boreal forests in continuous permafrost zone –
taiga. This proves the common knowledge that
the altitudinal and latitudinal gradients are very
similar. Berretti et al. (2004), Gubka (2004) and
Kucbel et al. (2008) reported that approximately
one half of mountain forest stands have homo-
geneous single-storied structure. In our case,
there is a tendency towards a less differentiated
height structure in the third and the fourth el-
evation category.

Conclusion

The analysis of the height structure of moun-
tain spruce forests in the nature reserve Babia
hora, Slovakia revealed a close relationship be-
tween maximum tree height and elevation (cor-
relation index equal to 0.91), as well as between
tree height and tree diameter (correlation index
varied from 0.93 to 0.99). For Norway spruce
(Picea abies L.), height-diameter relationship
was described by a five-parameter exponential
function, because simpler functions were not
able to represent the small values below the
usual truncation point satisfactorily. In case of
rowan (Sorbus aucuparia L.), Gompertz function
was used for the description of height-diameter
relationship. The results of tree height frequen-
cies indicated that the most differentiated verti-
cal structure is in the stage of growth. The stage
of breakdown is characterised by bimodal dis-
bution. With increasing elevation the differ-
ences between the vertical structure of the stage
of optimum and breakdown diminish, while
the differences between the stage of growth and
the stages of optimum and breakdown become
more distinct.

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References
Svoboda, M. 2005: Struktura horského smrkového lesa v oblasti Trojmězné ve vztahu k historickému vývoji a stanovištním podmínkám [Structure of the mountain spruce forest in the area of Trojmězná Mt. related to the historical development and site conditions]. Silta Gabreta, 11(1): 43–62.