ORIGINAL PAPER

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Altitudinal variability of stand structure and regeneration in the subalpine spruce forests of the Pol'ana biosphere reserve, Central Slovakia

Abstract The structure of natural subalpine spruce forest in the Zadná Pol'ana massif of the Western Carpathians was analysed. We focused on the variability of different aspects of stand structure, tree decay and regeneration processes in altitudinal gradient. We used systematic sampling, covering an area of 2 km^2, to detect even subtle changes in stand structure within one forest type over a range of less than 200 m in elevation. Mean stand density was 290 trees (> 7 cm DBH) per hectare, average basal area was 41 m^2 ha^{-1}, and the volume accumulation in living trees amounted to 500 m^3/ha^{-1}. Stand volume decreased by more than 50% between 1,260 and 1,434 m a.s.l. This means for an increase of altitude of 100 m that stand volume decreased by nearly 200 m^3. Neither stand density nor basal area was related to elevation. Maximum tree height was strongly correlated to elevation, and it decreased on average by 6 m for each 100 m increment of altitude. No significant changes in the maximum spruce diameter were recorded in relation to the elevation gradient. Spatial distribution of trees was biased toward regularity at lower altitudes. Tree clustering increased with increasing altitude. The stock of coarse woody debris (CWD) decreased slightly along the altitudinal gradient, but changes were not significant. Density of spruce saplings and their number growing on CWD significantly increased across the elevation gradient. Despite the fact that the analysed forest tract was relatively large, highly variable in respect to environmental factors, and that stand volume, spatial structure, and tree height displayed strong variability along the elevation gradient, the diameter structure of stands and regeneration measures were uniform. Our results suggest that the recruitment of new trees in the Zadná Pol'ana subalpine spruce forest is not temporally continuous even at a scale of several square kilometres.

Keywords Altitudinal gradient · Coarse woody debris · Natural regeneration · Old-growth forest · Western Carpathians

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Introduction

Processes shaping the spatial patterns of forests are highly dependent on local environmental conditions. Among these, climate and soil conditions are often very important and their gradients are responsible for structuring forested landscapes. Even at small spatial scales (i.e. several hectares) a large number of forest types can often be distinguished, resulting from short-distance changes in water availability, as well as in the physical and chemical properties of soil (e.g. Chytry and Spribille 2002; Pedrotti 2004). Climate, as a factor shaping the variability of forest vegetation has mostly been investigated over much larger spatial scales, such as phytogeographical zones or mountain vegetation belts. Numerous studies carried out over large areas demonstrated the close relationship between climate and fire regime (Veblen et al. 2000; Bekker and Taylor 2001; Clarke et al. 2005). However, much less attention has been paid to the climatic variation as a factor involved in forest dynamics within small spatial extent (Boose et al. 1994; Kulakovski and Veblen 2002). Such studies are particularly feasible in mountain areas, where topographical factors play an important role. Modifications

of stand structure along steep altitudinal gradients and on various slope aspects may result from changes in tree growth rate, tree morphology, disturbance regimes and regeneration processes. These traits have already been analysed along altitudinal gradients (e.g. Lieberman et al. 1996; Tang and Ohsawa 1997; Barrera et al. 2000; Wang et al. 2004). However, extensive ranges of altitude have been considered in such studies, and it is not surprising that ecological processes and forest structures differ considerably between distant sites.

Forest structure can be divided into various components such as the spatial distribution of trees, tree density, diameter, and height differentiation (Zenner 1999). For the description and quantification of structural diversity, various methods can be used from the descriptive to diverse graphic methods. These characteristics are very simple to collect in the field, however their information content is fairly low. For the comparison of different forest structures, various kinds of structural indices are used, which have high information content (Clark and Evans 1954; Cox 1971; Albert et al. 1995; Jaehne and Dohrenbusch 1997; Gadow et al. 1998; Jimenéz et al. 1998). Complex indices that include two or more components of structural diversity are often used, particularly those by Pretzsch (1996, 1998), Jaehne and Dohrenbusch (1997), Lähde et al. (1999) and Zenner (1999).

In Central European mountains extensive remnants of old-growth subalpine spruce forests remain only in the Carpathians. In the Alps, grazing and forestry have heavily impacted subalpine forests for centuries (Cherubini et al. 1996; Bebi et al. 2001). Even the best-preserved subalpine coniferous forests bear clear signs of previous wood exploitation and shepherding (Motta et al. 2002; Risch et al. 2004). On that account, remnants of Carpathian old-growth forests are of great value for studies on forest changes in strong environmental gradient as they have been well preserved within their whole elevation range in many localities.

The aim of our study was to identify spatial patterns in the structural and functional characteristics of subalpine spruce forests within the relatively narrow altitudinal range in the Pol'ana Biosphere Reserve. We focused on the spatial variability of different aspects of stand structure, tree decay and regeneration processes. We hypothesized that (1) stand structure and tree morphology change with altitude due to pronounced climate variation, (2) the amount of deadwood (a) increases with altitude as the rate of decomposition decreases with climate cooling (Kueppers et al. 2004) or (b) decreases in altitude as it is directly related to the site productivity and stand biomass (Siitonen 2001; Nilsson et al. 2002) that decreases with elevation, (3) *Picea abies* regeneration decreases with altitude as demands of young spruces for light increases in the altitudinal gradient (Pisek and Winkler 1959). Some of the above relationships have already been examined (Myczkowski 1964; Vacek 1982; Wojterski et al. 1982; Vacek and Podrázský 1998; Srutek et al. 2002). The

small numbers of measured stands was an important deficiency of these studies and this could bias the spatial patterns revealed in the studies. In our investigations, we used more intensive and systematic sampling covering an area of 2 km^2 to detect even subtle changes of stand structure within one forest type over a range of less than 200 m in elevation.

Materials and methods

Study area

Subalpine spruce forests of the Western Carpathians are distributed over several mountain ranges in Slovakia, Poland and the Czech Republic. In total, they cover an area exceeding 1,000 km^2 and dominate at elevations from roughly 1,100 to 1,600 m a.s.l., depending on geographic locality. High altitude tree stands in the Zadná Pol'ana massif are nearly exclusively built by *Picea abies* accompanied by *Sorbus aucuparia*. Small areas of *Acer pseudoplatanus* can develop in these forests on more fertile soils. In the shrub layer, spruce and rowan saplings dominate with some *Lonicera nigra*. Ground vegetation is usually formed by one strong dominant, *Vaccinium myrtillus*, *Athyrium filix-femina*, *Calamagrostis villosa* or *Dryopteris dilatata*. According to Zlatnik (1959), these forests represent two associations: *Sorbeto-Piceetum* on flat areas and gentle slopes with less fertile soils and lower pH, and *Acereto-Piceetum* on steeper slopes with more fertile soils. They extend from about 1,300 m a.s.l. up to the top of Zadná Pol'ana.

The old-growth stands in the upper part of the Pol'ana range are especially interesting, with respect to the aim of our study, as they represent the southernmost extent of subalpine spruce forests in the Western Carpathians (Korpel' 1995). They have been preserved in a nearly natural state and no large-scale timber exploitation took place in this area. The only known human intervention in the past was associated with sheep grazing in subalpine meadows, which were created by cutting and burning the woods along the mountain ridges. In meadows, single trees (usually the smaller ones) were cut for fuel wood and for construction timber. The grazing activity in Pol'ana region ceased in the middle of twentieth century. A 686 ha nature reserve was established in 1972. In the year 1990, the whole massif was taken under protection as a Biosphere Reserve covering the area of 20,100 ha.

The massif of Pol'ana is situated in central Slovakia, about 30 km east of the city of Banska Bystrica. It is a typical inactive stratovolcano with the main crest surrounding the caldera and reaching 1,458 m a.s.l. It consists of augitic-hyperstenic to hyperstenic andesite with less solid tuffs and tufaceous rocks. The dominant soils are andosolic cambisols and cambisolic andosols. Other soil types, present to a lesser extent, have devel-

oped including andosolic ranker, psephitic and pseud-ogleyic cambisols (Kukla 1995).

The climate in Pol'ana range is affected by warm air masses coming from the Pannonian plain. These air masses make the summer temperatures higher than in other high mountain ranges of the Western Carpathians (Korpel' 1995). At meteorological station Pol'ana chata (1,264 m a.s.l.), the annual mean temperature is 3.7°C, the warmest month is July with an average temperature of 12.8°C, annual precipitation is 1,069 mm, and there is snow cover for approximately 180 days. Using an extrapolation method, it was established that in the highest part of the massif (at 1,400 m a.s.l.), mean annual temperature is between 2.5 and 3.0°C, annual precipitation is 1,105 mm, and snow cover lasts 188 days (Škvarenina et al. 2004).

Data collection

In 2002, we established a set of regularly distributed circular sample plots with a radius of 12.6 m and an area of 0.05 ha each. The plots were spaced 200×200 m and covered the entire subalpine forest belt around the Za-dna Pol'ana peak over an area of nearly 200 ha. Location of each plot in the field was achieved using a portable GPS device. In total, we established 45 plots with the following altitudinal distribution: 13 plots at 1,250–1,300, 14 plots at 1,301–1,350, 13 plots at 1,351–1,400, and 5 plots at 1,401–1,450 m a.s.l. The lowest plot was located at 1,260, while the highest was at 1,434 m. The length of altitudinal gradient was 174 m.

Within each plot, we mapped and measured all living trees and snags with DBH > 7 cm, and stumps taller than 0.5 m. Tree mapping was conducted by measuring the azimuth and distance from the plot centre with the accuracies of 1° and 0.1 m. For each living tree, we measured DBH to the nearest cm and height with the accuracy of 0.5 m. For standing dead trees (snags), only DBH was measured.

For downed logs, we mapped and measured all the pieces exceeding a diameter of 7 cm situated within the circular plot boundaries. Because in most cases a considerable part of the downed logs was outside the plot boundaries, we measured only those parts within the plot boundaries, regardless if their stem base was located within the plot or not. According to the degree of wood decomposition, logs were assigned to one of eight decay classes (Holeksa 2001). Class I represented fresh fallen dead logs with intact branches, while class VIII was almost totally decomposed, with remnants of logs hardly visible on the forest floor. Each piece of coarse woody debris (CWD) was ascribed to a single decay class.

Tree seedlings ($\leq$ 30 cm tall) were measured at each plot in 10 quadrates of 1 m^2, distributed in 10 directions every 36° at 6.3 m from the plot centre. Saplings (> 30 cm tall, but less than 7 cm in DBH) were measured on the entire 0.05 ha plots. Saplings were divided into two height groups: 30–130 and above 130 cm up to a DBH of 7 cm. For each seedling and sapling, one of four microsites was recorded: soil, rock, windthrow mound, or dead wood. In total, seedlings and saplings were measured over areas of 450 and 22,500 m^2, respectively.

Data analysis

Calculation of stand parameters. Based upon the field measurements, we calculated the number of trees, stand basal area and stand volume for each plot. The latter was calculated as the sum of the volumes of individual trees. Tree volume V_t was computed according to the formula:

$$V_t = GHF, \tag{1}$$

where G basal area of a given tree, H tree height, F taper coefficient, assumed to be 0.45 for spruce and 0.65 for broadleaved trees.

The volume of downed logs V_l was estimated assuming a conical shape of logs according to the formula:

$$V_l = \frac{\pi(r_{\min}^2 + r_{\max}^2)}{2} l, \tag{2}$$

where is the $r_{\max}$, $r_{\min}$ respective diameters on both ends of a log, with $r_{\min} \geq 7$ cm, l length of log.

The data were collected from 45 sample plots distributed relatively uniformly over the elevation range from 1,260 to 1,434 m. This design allowed for a number of statistical analyses. One such analysis employed linear regression to evaluate possible relationships between elevation and various tree and stand parameters.

Analysis of stand structure. For the analysis of forest structure, two indices were used, the Clark–Evans index (Clark and Evans 1954) and the complex stand diversity index by Jaehne–Dohrenbusch (1997). The Clark–Evans Aggregation Index characterizes the horizontal tree distribution pattern by the relation of the observed average distance of all trees to their respective nearest neighbours to the average distance expected under a random spatial distribution. Its mathematic definition is:

$$R = \frac{\frac{1}{n}\sum_{i=1}^{n} r_i}{0.5\sqrt{\frac{n}{A}}}, \tag{3}$$

where r_i is the distance of tree i to its nearest neighbour, n number of sampled trees, A area of sample plot (in our case 500 m^2).

This index ranges from 0 for maximum clustering to 2.149 for a regular hexagonal tree distribution pattern. Values above 1 indicate a tendency to a regular distribution, while values below 1 indicate a tendency to clustering.

For practical purposes, it is not sufficient to just determine the index value, i.e. whether the distribution is random, or tends toward clustering or regularity, because in nature most of the variables have a stochastic character. Therefore, we need to know the level of significance of the difference between the calculated index value and the value corresponding to a random distribution. A *t*-test was used to determine if the difference between the observed index value and that expected for a random distribution was significant:

$$t = \frac{r_R - r_T}{\frac{0.26136}{\sqrt{n\frac{n}{A}}}}, \qquad (4)$$

where r_R is the observed nearest neighbour distance, r_T theoretical nearest neighbour distance, n number of sampled trees, A area of sample plot (here 500 m^2).

The stand diversity index B (Jaehne and Dohrenbusch 1997) consists of four variables of stand structural diversity: A tree species composition index, S vertical diversity index, V spatial distribution index and K tree differentiation index. Gadow (1999) quantified the first three variables. The index (B) has the following formula: $B = pA + qS + V + K$ where: p, q are weighting factors ($p = 4$, $q = 3$). Jaehne and Dohrenbusch (1997) described the detailed calculation of the indices.

Results

Stand characteristics

Average stand density was 290 trees per hectare. The coefficient of variation (CV) for tree number per plot was 44.9%. The average basal area was 41 m^2 ha^{-1}, and the CV was 32.6%. The volume accumulation in live trees amounted to 500 m^3 ha^{-1} on average and the CV was 47.7%. About 92% of the living trees were *Picea abies* (Norway spruce). The share of *Sorbus aucuparia* (rowan) was 3.7%, *Acer pseudoplatanus* (maple) 2.9, and *Fagus sylvatica* (beech) 1.7%. In terms of volume, the dominance of spruce was even more pronounced, as it constituted 95% of stand volume.

A very strong relationship was found between stand volume and maximum tree height recorded on the individual plots ($r = 0.83$, $P < 0.001$). Maximum height alone explains as much as 67% of the volume variability. Somewhat lower, but still significant, was the dependence of stand volume on maximum tree diameter ($r = 0.68$, $P < 0.001$). According to the multivariate regression model, both these independent variables explained 74% of the variability in stand volume.

Average DBH was 37.3 cm for all living trees, 38.4 cm for spruces, and 24.9 cm for deciduous trees. The maximum (and average) diameters for deciduous trees were: 60 cm (28 cm) for maple, 32 cm (16 cm) for beech and 31 cm (16 cm) for rowan. On individual plots, the maximum spruce diameter ranged from 42 to 110 cm. Over the whole massif, spruces below 15 cm
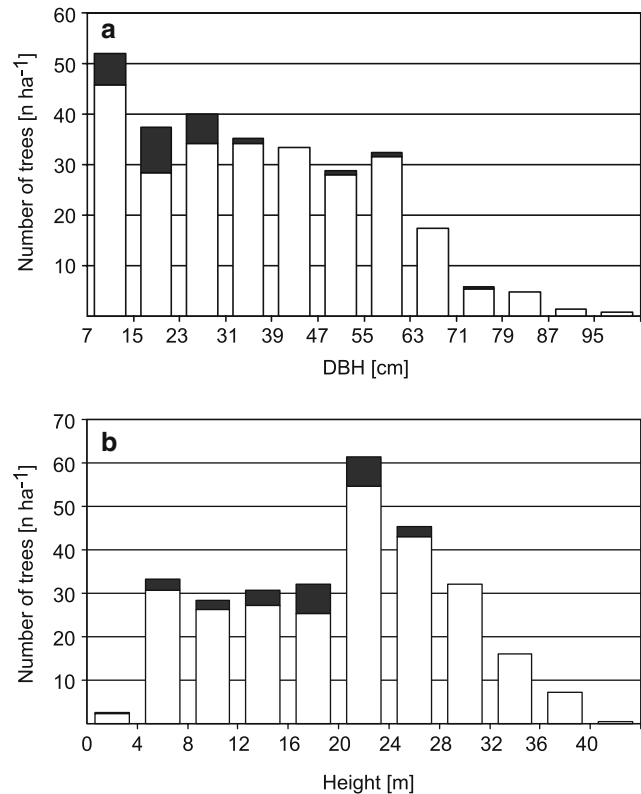

Fig. 1 Diameter (**a**) and height (**b**) distributions of living trees over the whole area of the subalpine spruce forest in the Pol'ana massif; spruce *light bars*, deciduous trees *dark bars*

DBH were most numerous, while the following diameter classes up to 60 cm were of nearly equal size (Fig. 1a). Among the deciduous trees, individuals between 15 and 23 cm DBH were most numerous.

The most abundant height class was between 20 and 24 m. The height distribution differed from the diameter distribution (Fig. 1b). The tallest tree recorded in the sample plots was 41 m, while the height of the shortest trees (among those with DBH at least equal to 7 cm) was only 2.7 m. All of the tallest trees in all samples were spruces. For individual plots, maximum height ranged from 22 to 41 m. Broadleaf species was clearly of lower stature. The tallest maple was 28, rowan 23, and beech 22.5 m. The mean height for beech (11 m) was lower than for rowan (16 m) and indicated that in the subalpine stands of Pol'ana range, this species occurred only in the understory.

Coarse woody debris (CWD)

The average number of snags was 103 per hectare. The variability in the number of snags among plots was high (CV = 121.2%). The average volume of snags and stumps amounted to 48.6 m^3 ha^{-1} with a CV of 127.6%. Spruce snags dominated, as they constituted over 97% of the number of snags and almost 99% of their total volume. The diameter distribution of the snags was

significantly different from that of living trees (Kolmogorov–Smirnov test, $D = 0.39$, $P < 0.001$). It was more positively skewed, with a conspicuous dominance of thin specimens below 20 cm (Fig. 2a). The average DBH for snags was only 24.4 and the median was 17 cm.

The average number and volume of logs were 181 pieces and 94.9 m^3 ha^{-1}. Spruce logs contributed 94% of this volume, while 6% belonged to logs of deciduous trees (mostly to rowan, 4%). The variability in the volume of logs was in between those for living trees and snags (CV = 88.3%).

The diameter distribution of logs differed slightly, but significantly, from that of snags (Fig. 2b; Kolmogorov–Smirnov test, $D = 0.11$, $P < 0.05$) and differed considerably from that of living trees (Kolmogorov–Smirnov test, $D = 0.43$, $P < 0.01$). The average DBH of logs was 20.5 cm. It was 17 cm less than DBH of living trees and 4 cm less than DBH of snags. The most abundant was decay class I with nearly 25 m^3 ha^{-1}, followed by class II (17.7 m^3 ha^{-1}). There was very little variability among decay classes III–VII: all of them contained from 6.6 to 11.1 m^3 ha^{-1}. The least dead wood, about 0.5 m^3 ha^{-1}, was found in decay class VIII (Fig. 3).

The total number of snags and logs was slightly higher than the number of living trees (294 vs. 290 per ha). The volume of stumps, snags and logs was
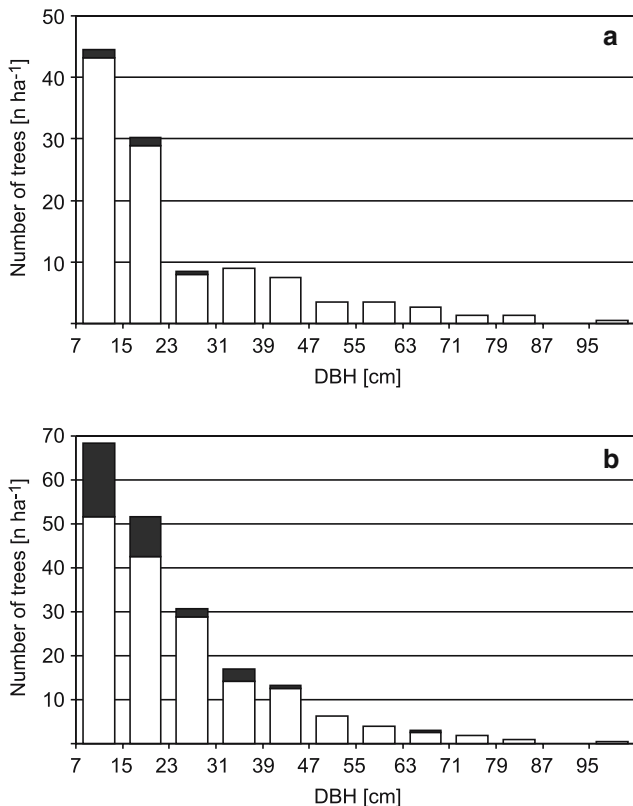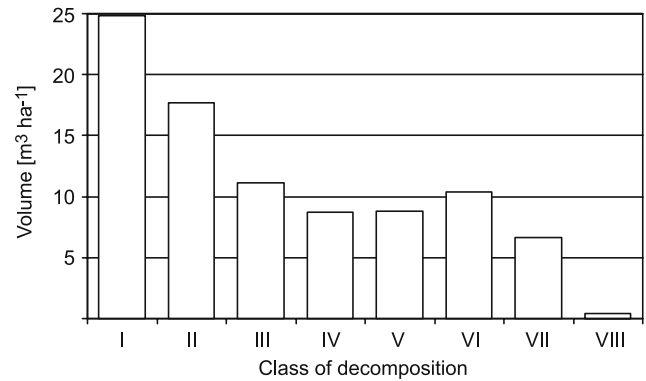

Fig. 3 Distribution of log volume in eight decomposition classes

143.5 m^3 ha^{-1} and the proportion of CWD volume in total volume of living and dead trees was 24%.

Tree regeneration

Seedlings of three species and saplings of four tree species were present on 45 plots. *Picea abies*, *Sorbus aucuparia* and *Acer pseudoplatanus* were noted in both groups, while *Fagus sylvatica* was found only among saplings. The number of seedlings was highly variable between sampled plots and their average density was 7.9 individuals per 10 m^2, corresponding to 7,867 individuals ha^{-1}. The number of saplings was also very variable between plots with average density of 1,626 individuals per hectare. As much as 91% of the seedlings and 96% of the saplings belonged to Norway spruce and rowan. The density of spruce seedlings was 3,956, and 3,200 individuals ha^{-1}, for rowan. Most spruce seedlings (80%) and rowan seedlings (62%) were shorter than 10 cm. Spruce and rowan yearlings were rare. Their densities were 110 and 440 individuals ha^{-1} respectively. Total density of spruce saplings was 92 individuals ha^{-1}, while it was 16 times higher for rowan, with a value of 1,465 individuals ha^{-1}.

Most spruce seedlings (75%) and saplings (50%) grew on undisturbed soil. As much as 17% of seedlings and 32% of saplings were found on coarse woody debris. Stones and windthrow mounds supported 8 of seedlings and 18% of saplings, respectively.

Changes of tree stand characteristics along the altitudinal gradient

There was a tendency towards a decrease of living tree volume with increasing elevation (Fig. 4a). Pearson's correlation coefficient between elevation and stand volume amounted to 0.37 ($P = 0.012$). This was the only tree stand characteristic significantly related to elevation. Neither the density nor basal area of living trees was related to elevation. The linear regression calculated for stand volume as dependent on altitude revealed that

Fig. 2 Snag (**a**) and log (**b**) diameter distributions over the whole area of the subalpine spruce forest in the Pol'ana massif; spruce *light bars*, deciduous trees *dark bars*
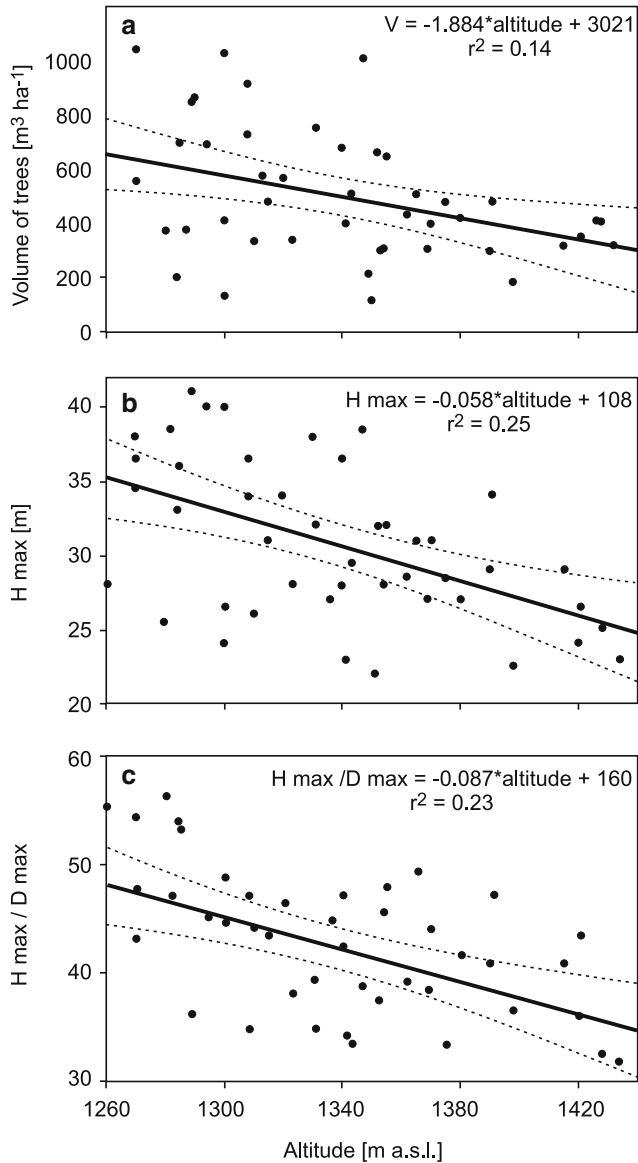
Fig. 4 Relationships between altitude and stand volume (**a**), maximum tree height (**b**) and the index of trunk slenderness (**c**)

in the analysed gradient, between 1,260 and 1,434 m, volume decreased by more than 50% from 665 to 321 m^3 ha^{-1}. Thus, for an increase of altitude by 100 m, volume dropped by nearly 200 m^3.

Maximum tree height was strongly negatively correlated to elevation (Pearson's correlation coefficient $r = -0.52$, $P < 0.001$). Regression analyses showed that for each 100 m increment of altitude, maximum spruce height decreased by 6 m. The tallest spruces, exceeding height of 40 m, were found only in low-elevation subalpine forests, below 1,300 m a.s.l. In the highest part of the Pol'ana Biosphere Reserve, above 1,400 m a.s.l., the tallest recorded spruces attained 29 m (Fig. 4b).

The index of trunk slenderness (defined here as a maximum tree height within a plot divided by the maximum tree diameter in the same plot, but not

necessarily in the same tree) was also strongly and negatively correlated to elevation (Pearson's correlation coefficient $r = -0.50$, $P < 0.001$). For each 100 m increment of altitude, the index of trunk slenderness dropped by 8.7, i.e. from 50.4 at 1,260 m to 35.2 at 1,434 m a.s.l. (Fig. 4c). However, there was no significant relationship between altitude and maximum spruce diameter (Pearson's correlation coefficient $r = -0.05$, $P = 0.74$)

Density and volume of CWD decreased slightly along the altitudinal gradient, but changes were not significant. There was also an insignificant relationship between elevation and the proportion of CWD to total volume of living and dead trees. This proportion was slightly higher in the upper part of the gradient.

Norway spruce stands in the altitudinal zone below 1,300 m were characterized by the highest values of the Clark–Evans index ($R = 1.20 \pm 0.16$; mean $\pm$ SD). This result indicates that in the lower portion of the studied altitudinal gradient, the distribution of trees was biased significantly toward regularity. With increasing altitude, the index became lower, and smallest values were found above 1,400 m ($R = 0.92 \pm 0.20$), showing a tendency for tree clustering, albeit this was not significant (Fig. 5a).

The Jaehne–Dohrenbusch index B of stand diversity indicated low diversity of spruce stands along the whole gradient (Fig. 5b). It ranged between 3.2 and 4.8. The
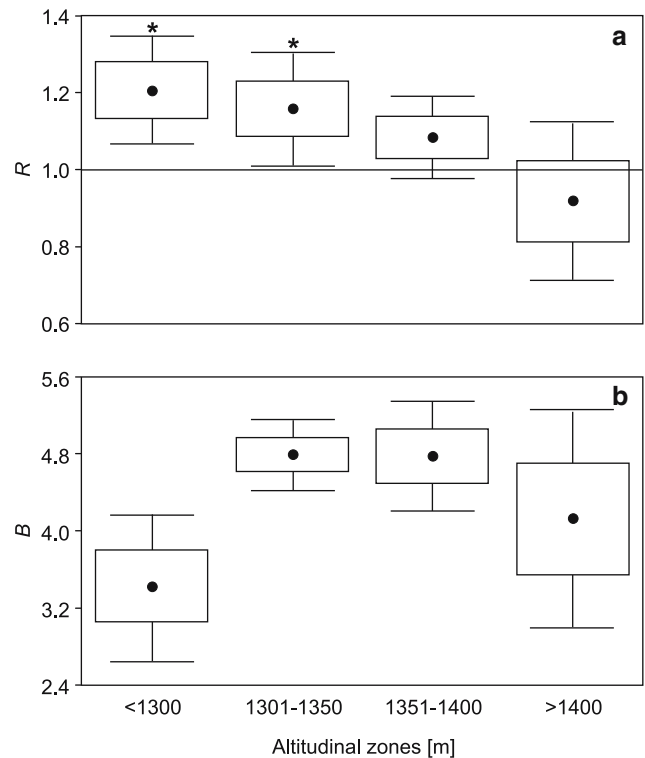

Fig. 5 Values of the Clark–Evans index R (**a**) and the Jaehne–Dohrenbusch index B (**b**) in Norway spruce natural forest NNR Pol'ana according to altitudinal zones. *Asterisks* denote significant departures from random trees distributions

least diverse ware stands located at low altitudes, while the highest diversity, which was still relatively low, was found in the middle portion between 1,300 and 1,400 m a.s.l.

The abundance of tree regeneration was related slightly to altitude. Seedlings of all tree species were distributed independently of altitude. The only significant and positive correlations with altitude were for spruce saplings, with their total number and the number of saplings growing on CWD (Fig. 6, Table 1).

Discussion

Compared to subalpine spruce forests in other parts of the Western Carpathians, tree stands in the Pol'ana Biosphere Reserve are characterized by a relatively high volume (500 m^3 ha^{-1} on the average). It is more than in all natural subalpine stands sampled in the Tatra and Beskidy mountains, where the accumulation of wood volume ranged between 150 and 496 m^3 ha^{-1} (Jagiełło et al. 1978; Korpel' 1995; Holeksa 1998; Chwistek 2001; Saniga 2002; Holeksa and Zielonka 2005). This is also higher than in the best preserved subalpine forests of the Alps (Mayer and Ott 1991) and in old-growth boreal spruce forests (Kuuluvainen et al. 1998; Siitonen et al. 2001; Rouvinen and Kouki 2002). Only in small plots of 0.5–1.0 ha representing the optimal phase of stand development, the volume may be still higher than in Pol'ana (Korpel' 1989; 1993; Mayer and Ott 1991). The average wood volume in subalpine spruce forests in Pol'ana is actually more similar to the mean values recorded in old-growth mixed mountain forests of lower elevations (Korpel' 1995; Holeksa et al. 2004). Moreover, the volume recorded in the lower part of the gradient, below 1,300 m a.s.l. (> 600 m^3 ha^{-1}) is higher than in many mixed mountain forests.

It is essential to note that the lower distribution limit of subalpine spruce forests in the Pol'ana range (1,250–1,300) is situated substantially higher than in the Beskidy mountains (1,100–1,150) or the Tatra mountains
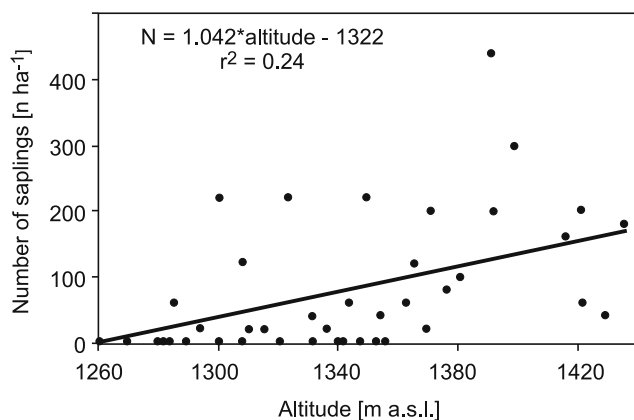
(1,200–1,250 m a.s.l.). As the Pol'ana range is the southernmost range of the Western Carpathians, its climate is warmer and milder than in the north Carpathians, and the sum of precipitation is lower. This explains the altitudinal shift in forest belts, but not necessarily the higher biomass accumulation in the Pol'ana spruce forests. The latter is probably due to the fact that the soils in Pol'ana range, developed from the andesite bedrock, are characterized by a high fertility and a large water-holding capacity. This represents an advantage in comparison with soils developed from Carpathian flysch, mainly sandstones, in the Beskidy mountains or from granites in the Tatra mountains.

In spite of high average stand volume in Pol'ana range, the value recorded above 1,400 m a.s.l. is among the lowest in the West Carpathian subalpine forests. This result is interesting as in most West Carpathian ranges; spruce forests reach their upper limit at higher elevations than the elevation of the Pol'ana summit. In the Tatras, Nizke Tatry, Mala Fatra and Velka Fatra mountains, the upper limit is usually between 1,500 and 1,600 m a.s.l. (Michalko et al. 1986). Only at the northernmost localities in the Babia Góra and Pilsko massifs is the upper forest limit situated around 1,400 m (Celiński and Wojterski 1978). Thus, it can be assumed that altitude is not the only cause in the reduction of stand volume in the uppermost part of Zadná Pol'ana. Rather decrease of stand volume likely results from a topographical factor, namely sites close to the ridge are exposed to strong winds, which may constrain the growth of trees.

Subalpine forests of the Pol'ana massif are an excellent example of the prevailing influence of climatic factors on high mountain localities. In this study, the change of climatic factors in the elevation gradient affected tree size and stand structure. Elevation is the single most important factor explaining much of the variability in maximum tree heights, tree slenderness, and total stand volume. Contrary to the strong relationship between altitude and spruce height, maximum spruce diameter was not related to this factor. This confirms the results of other studies in which diameter is not very sensitive to changes in elevation (Lieberman et al. 1996; Barrera et al. 2000; Paulsen et al. 2000; Srutek et al. 2002).

The amount of CWD recorded in the subalpine spruce forest of Pol'ana is among the highest measured in Carpathian spruce forests (Korpel' 1989, 1993; Jaworski and Karczmarski 1995; Saniga 2001). Data on CWD from most natural subalpine forests of the Alps showed much lower values (Utschick 1991; Albrecht et al. 1993; Derleth et al. 2000). Also in boreal old-growth spruce forests, the amount of CWD is usually lower than in the spruce mountain forests of Western Carpathians (Linder and Östlund 1992; Linder et al. 1997; Kuuluvainen et al. 1998; Jonsson 2000; Mattias and Jonsson 2001; Siitonen 2001; Storaunet and Rolstad 2002). The great amount of CWD in Pol'ana Biosphere Reserve, and particularly about 20 m^3 ha^{-1} of well-de-

Fig. 6 Relationship between altitude a.s.l. and density of spruce saplings

Table 1 Results of statistical analysis of relationship between altitude and regeneration intensity

Dependent variable	R	P
Seedlings		
all seedlings	−0.16	0.29
Acer pseudoplatanus	−0.14	0.36
Picea abies	−0.19	0.21
Sorbus aucuparia	0.03	0.84
Saplings		
all saplings	−0.02	0.90
Acer pseudoplatanus	−0.05	0.74
Fagus sylvatica	0.08	0.60
Sorbus aucuparia	−0.05	0.74
Picea abies saplings		
***Picea abies* all saplings**	**0.61**	**< 0.001**
***Picea abies* saplings on CWD**	**0.46**	**0.001**
Picea abies % of saplings on CWD	0.15	0.50

In all cases, the Spearman rank correlation coefficient (*r*) was calculated. Significant relationships are marked with bold letters

cayed logs (classes VI–VIII) suggests that the extraction of timber has been low for long time and that the forest is well preserved in a nearly natural state.

The amount of CWD slightly decreased with increasing altitude, but the proportion of dead biomass (CWD) to total biomass (live biomass + CWD) increased slightly. However, both the trends were not significant. This suggests that the effects of variation among sites in productivity and in the rate of dead wood decomposition cancel each other along the gradient. One could expect that the strong decrease in stand volume along the gradient would produce a more pronounced trend in the proportion of CWD to total wood biomass. Weak relationships between CWD parameters and elevation probably result from high variation in the amount and proportion of dead wood, which are almost twice as great as the variation in number and volume of living trees. Our results do not confirm the strong and positive relationship between the amount of CWD and elevation found by Kueppers et al. (2004) in subalpine forests in Colorado, USA. However, Kueppers et al. (2004) considered a much wider range of elevation and there were no changes in stand biomass along the elevation. Systematic data on CWD amount has not been collected in boreal spruce forests, but compilation of numerous studies revealed that the amount of CWD decreases strongly northwards (Siitonen 2001).

Our results weakly confirm the well-known higher tendency for clumping of trees in spruce stands at higher altitudes, especially close to the upper forest limit (Vacek 1982; Doležal and Šrůtek 2002; Vorčak 2005). However, it should be mentioned that a regular distribution of trees in subalpine forests were only rarely observed. Trees were usually scattered randomly or their clumped distribution was pronounced. One point worth noting here is that our sampling was strictly regular across the whole massif, while in other studies a more subjective sampling design may have played a role in the final location of sample plots.

The diversity index by Jaehne and Dohrenbusch (1997) indicated a low diversity of spruce stands along the whole elevation gradient. The lowest diversity was recorded at lower elevation. This is understandable, since the regeneration process is very weak, especially at elevations below 1,400 m a.s.l. Carpathian subalpine spruce forests are among the least diverse in respect of species composition and structure (Jaehne–Dohrenbusch diversity index was between 3 and 5). For instance, much higher values of the Jaehne and Dohrenbusch diversity index ($\approx$ 7) were recorded in two managed subalpine stands in the Austrian Alps at 1,490 and 1,540 m a.s.l. (Neumann and Starlinger 2001).

The average density of spruce saplings noted in this study was very low. Moreover, the spatial distribution of saplings was highly clustered, and many plots at lower altitudes were devoid of spruce saplings. Only in the highest part of the massif did the density of saplings exceed 200 individuals per hectare. The increase of the density of spruce saplings with increasing altitude was the only significant relationship. This finding contradicts our hypothesis that assumed increased light requirements and a decrease in the density of young spruces in the elevational gradient. As stand density is similar across the whole gradient, it seems that changes in the spatial structure of stands could be responsible for altitudinal variation in the recruitment of spruce saplings. Changes from a regular distribution of trees at low elevation through random to the tendency for clumping in the highest part of the gradient cause probably better light conditions on the forest floor at higher altitudes. The average interception of light depends on the spatial distribution of trees. It is greater in a stand with regularly distributed trees than in stand with trees randomly distributed (Oker-Blom and Kellomäki 1983). At higher altitudes, areas occupied by tree clumps adjoin to places free of trees. This creates a high spatial variation in light conditions with shaded areas under tree clumps and light reaching the ground outside of the clumps of trees (Kuuluvainen and Pukkala 1987).

Contrary to the low sapling density, the seedling bank was abundant along the elevation gradient. This bank consisted of almost 4,000 individuals ha^{-1}. Similar differences in the density of spruce seedlings and saplings were also recorded in another old-growth subalpine forest of the Western Carpathians, in the massif of Babia Góra, where the ratio between these two regeneration groups (excluding yearlings) was 20:1 (Holeksa 1998), compared to 42:1 for our studies. This suggests that in spite of the presence of an abundant seedling bank, spruce regeneration in subalpine forests is highly discrete in time with long periods of low recruitment of new trees. Extremely different results were obtained in boreal spruce forests were spruce saplings occur abundantly. Kuuluvainen et al. (1998) recorded almost 2,000 spruce saplings per hectare (> 30 cm in height) in the undisturbed taiga of the southern boreal zone near the Ural mountains. More than 1,000 saplings (> 50 cm in height) per ha were noted in small gaps in the old-

growth forest in central Sweden (Quinghong and Hytteborn 1991). Most probably, differences between boreal and subalpine forests in spruce sapling density stem from different light requirements of spruce saplings in both regions. It has been known for long that demands for light of *Picea abies* increases with altitude (Pisek and Winkler 1959) and they are especially high in subalpine forests.

Differences in spruce sapling density between subalpine Carpathian and boreal forests explain the high discrepancy between these forests in the diameter structure of stands. As advanced spruce regeneration is abundant in boreal forests, the recruitment of new trees is possible immediately in response to the formation of each new gap. In subalpine forests, a small number of saplings are insufficient for filling all new gaps. Numerous small seedlings shorter than 10 cm, that can persist several years under closed stands, have to compete with tall shrubs, ferns and grasses (Reif and Przybilla 1995) that also takes advantage of light conditions in gaps. Therefore, the chances of seedlings to become saplings and eventually reach the canopy level are extremely low even in case when large canopy gaps are formed.

Conclusion

Despite the fact, that the analysed forest reserve was relatively large, highly variable in respect to environmental factors, and that tree heights and stand volumes displayed strong variability along the elevation gradient, the structure of tree stands was quite uniform. This uniformity refers especially to the diameter distribution and the number of thin stems being much lower than expected if continuous recruitment of new trees could take place. At the same time, relatively thin stems were the most abundant among snags and logs in the Pol'ana range. This suggests that recently self-thinning has been a dominant process eliminating trees from spruce stands over the whole massif.

The size class distribution of *Picea abies* in subalpine forests along with small sapling density suggest that the recruitment of new individuals is not continuous even at large spatial scales ($> 1\ \mathrm{km}^2$), contrary to findings in boreal spruce forests where the recruitment of trees seems to be a continuous process even at small spatial scales (< 1 ha). We suspect, that the lack of continuous regeneration can be an important feature of subalpine spruce forest in the Carpathians, although the mechanism responsible for this phenomenon remains unclear. Most probable is that gap-phase regeneration due to high light requirements of saplings plays a minor role for this forest type. Subalpine spruce forests in the Western Carpathians seem to be shaped by large-scale disturbances, and even over a large spatial extent of several square kilometres their structure does not reach a state of quasi-equilibrium of tree recruitment and death.

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