

STAND DYNAMICS OF THE SUBALPINE SPRUCE (*Picea abies* L. Karst) FOREST – A DISTURBANCE DRIVEN DEVELOPMENT

SASTOJINSKA DINAMIKA PRETPLANINSKE ŠUME SMREKE (*Picea abies* L. Karst) – REZULTAT PRIRODNIH POREMEĆAJA

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Summary

The paper deals with the stand dynamics of subalpine Norway spruce forest in the Low Tatras Mts., Slovakia. The recent state of subalpine spruce forests is unsatisfactory because of the extensive windstorms followed by bark beetle outbreak. The study is focused on the reconstruction of historical disturbances affecting this locality in the past. The research was conducted on the model locality Mt. Veľký Bok in the Low Tatras, central Slovakia. After the harvesting of snags we cored spruce stumps (N=60). Boundary-line criteria (fig.1) were used for evaluation of growth releases. We reconstructed local disturbance chronology and tree recruitment chronology. Three distinctive peaks of growth releases were revealed, in 1860–1880; 1920–1940 and 1980–2000. The identified disturbance periods were confirmed by examination of historical sources. Regarding the tree recruitment patterns, 50 % of analyzed trees met the criterion of gap recruitment. The temporal position of recruitment waves fairly corresponds with occurrence of a major disturbance. According to obtained results, we can state that the large-scale wind disturbances are the natural part of subalpine spruce forest and the overall dynamics of investigated forest is driven by combination of gap and patch dynamics.

KEY WORDS: growth release, Norway spruce, boundary line, Central Europe, natural disturbances

Introduction

Uvod

In spite of small area extent of subalpine spruce forests these are of high importance regarding the numerous non-productive functions. Soil-protection, avalanche protection and securing of water supplies are only the fragment of functions that are provided by subalpine spruce forests.

Generally, the Norway spruce decline is caused by the synergistic influence of several natural and anthropogenic factors, whereby wind, snow, emissions, drought, nutrient

shortage, insects and fungi are considered the most important ones (Schmidt-Vogt 1989, Kucbel et al. 2004; Grodzki 2007). According to Kucbel (2000b), the recent state of protection forests in conditions of the Low Tatras Mts. can be characterized as a result of the combination of extreme environmental conditions as the low temperature, long lasting snow coverage, shallow soil etc. and anthropogenic impact (pasture and uncoordinated tree harvest, the impact of emissions, global warming). Homogenous structure and height leveling together with the anatomy and morphology of

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shallow root system creates preconditions to uprooting. Due to its shallow depth, the roots are often unable to stabilize the tree in soil on extreme steep slopes. Lack of silvicultural interventions resulted in dense forest structure where the process of auto-reduction and gradual reduction of crown make the individual static stability more susceptible to wind damage.

Despite all listed damaging factors, the wind disturbances are considered to be the crucial natural force driving the dynamics and development of subalpine spruce forests according to comprehension of many forest ecologists (e.g. White, Pickett 1985; McCarthy 2001; Splechna et al. 2005).

The main goal of this paper is to evaluate whether the large-scale wind and bark beetle disturbances are the phenomenon of the last decade, or if they are the ordinary part of subalpine spruce forest development in the conditions of Slovakia. Following tasks will be analyzed in detail:

1. Age structure and tree recruitment in time;
2. Intensity and periodicity of disturbances – reconstruction of disturbance regime;
3. Role of disturbances in development of forest.

Materials and methods

Materijal i metode

Site description – Opis staništa

The study was conducted in the Low Tatras Mts. Regarding the orography unit, the mountain range belongs to Western Carpathians. The research plots were established on the northern slope of the Mt. Veľký Bok. The elevation of the site ranges from 1450 to 1550 m above sea level, with NE aspect. The prevailing soil type is skeletal cambisol with the average depth to bedrock of 20 cm throughout the site. Typical mountain forest of the 7th vegetation altitudinal zone (group of forest types *Sorbeto-Piceetum*) is almost exclusively dominated by Norway spruce (*Picea abies* L. Karst) but tree species composition also includes less abundant tree species, such as silver fir (*Abies alba* Mill.) and rowan (*Sorbus aria* L.).

In the past, the set of permanent research plots (PRP) was established to capture the structural changes of subalpine forest ecosystem in this locality. However, after the bark beetle outbreak in 2010, the locality was completely harvested. Our study was focused on the dendroecological analysis of the stand dynamics as well as the reconstruction of disturbance regime. Following the approximate location of former research plots (location of plots was not GPS positioned) we established a 20×200 m transect ranging from the position of former lowest PRP toward the upper tree line.

Sample collection and processing –

Prikupljanje i obrada podataka

Transect was divided into 20×20 m subplots for systematic sampling. At each subplot approximately five stumps were cored (one core per stump) regarding the decay state of stump. Across entire transect we obtained the cores over a complete range of diameter classes. Following this procedure, also suppressed trees were included into analysis, because there was no opportunity to estimate the former height position of tree after it was cut. The perimeter of each sampled stump was recorded as well. All obtained increment cores ($N=60$) were air dried and sanded according to Cook, Kairiukstis (1996). Rotten and fragmented cores were excluded from further analysis. Rest of the samples was scanned using the Epson Expression 10000XL scanner and the ring widths were measured (WinDendro[®] software). In the cases the core missed the pith ($N=14$), we approximated the prior growth according to average width and curvature of five innermost rings. The tree ring series were crossdated according to marker year method (Yamaguchi 1991). We confirmed the accuracy of crossdating by COFECHA software (Holmes 1983). All crossdated series ($N=47$) were used for further analysis.

Data analysis – Analiza podataka

At first, all tree cores were inspected for the prospective gap origin. We calculated initial growth rates as the 5-yr average radial growth for each core at the point where the tree was 4 cm at sampling height. Result should be compared to threshold value assessed experimentally using the growth rates of suppressed and gap originated saplings at the site (Lorimer, Frelich 1989). In our case, all trees were cut therefore we used the threshold rate (1.93 mm year⁻¹) proposed in the work of Svoboda et al. (2012) for the ecologically comparable spruce stand in Šumava National Park. Trees that passed the given threshold were considered "gap established".

For the quantification of abrupt growth events, we calculated the percent-growth changes as a running comparison of sequential 10-yr annual ring widths (Nowacki, Abrams 1997). This approach allows discounting the short-term growth pulses caused by climate events and gradual change of growth patterns due to tree ageing. We were focused on positive growth releases that are considered to be the indicator of removal of overtopping canopy tree.

For evaluation of growth changes we followed the procedure proposed by Black, Abrams (2003).

Obtained growth changes were plotted with respect to prior growth values and boundary line recently developed for *Picea abies* by Splechna et al. (2005). However, the growth change data failed to reach the used boundary line at almost all levels of prior growth (Fig. 1, top) therefore we develo-

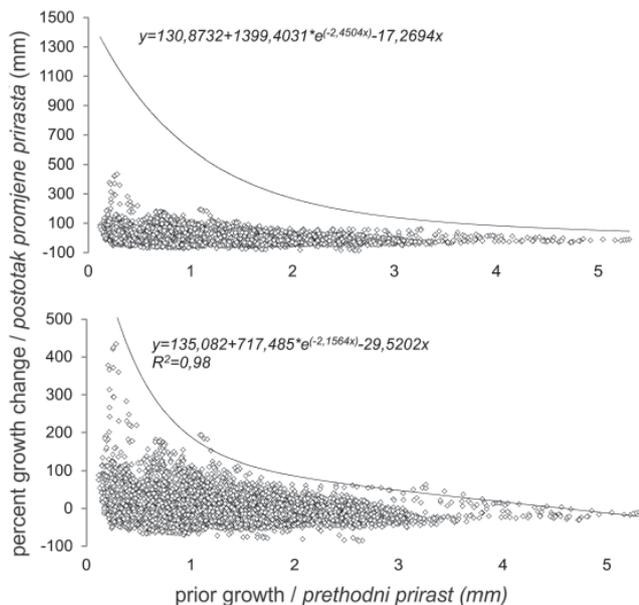


Figure 1. Boundary line constructed according to Splechtna et al. (2005) (upper) and local boundary line, $N=6008$ (lower) developed for Norway spruce in the LowTatras.

Slika 1. Granična linija konstruirana prema Splechtna et al. (2005) (gore) i lokalna granična linija, $N=6008$ (dolje) za običnu smreku u Niskim Tatrama.

ped the local boundary line using our collected samples. The upper threshold of the relationship between prior growth and percent-growth change was constructed using the procedure proposed by Black, Abrams (2004). We modified the method according to Nagel et al. (2007). The average of top ten values calculated for each 0.5 mm prior growth segment were fitted by the modified negative exponential function with additive linear term. The final boundary line yielded the highest R^2 value (Fig. 1, bottom). For the identification of growth pulses we used the threshold 10 % suggested by Black, Abrams (2003). The percent-growth changes that did not reach the given threshold were dropped from further analysis. Once the final boundary line (BL) was constructed, we scaled the maximum growth changes of each identified growth pulse as a fraction of the boundary line. The pulses were classified according to Black, Abrams (2003) as follows: below 20 % of the BL "no release – effect of climate"; 20–49.9 % "moderate release"; above 50 % "major release". The disturbance history is then expressed as a portion of trees showing the release event for each decade of chronology. For the reconstruction of vertical shifts of trees within the forest space we assessed the "canopy accession events" for each tree. Following Svoboda et al. (2012), the first major release was considered as a canopy accession. For some cases the moderate release could be used as an indicator of canopy entering but it has to be the first and only release during the life of tree. Rest of the trees that did not fulfill the criteria indicating the gap recruitment was sorted with respect to their overall growth pattern (Lorimer, Frelich 1989, Svoboda et al. 2012).

Results Rezultati

In studied sample, a relatively high variability regarding the individuals age was recorded. The age of sampled spruces ranged from 47 to 226 yr with the mean age of 145 ± 50 yr. Diameter structure was relatively homogenous, with the average diameter of 41.9 ± 13.9 cm. When the age-diameter relation was examined, the regression analysis showed a quite weak relationship ($R^2=0.49$, $p=0.001$) (Fig.2, top).

Regarding the recruitment of spruce trees, the analysis exhibited the fairly continuous recruitment during the whole studied period, except the decades 1790 and 1920 (Fig. 2, bottom). We recorded three periods of high tree recruitment: 1800–1830 (34 % of all sampled trees), 1860 (12 % of trees during one decade) and 1910–1930 (25 % of all recruited trees). The analysis confirmed one period of low tree recruitment (1880–1900) and a decreasing tendency in tree recruitment in the period since the 1940 that is dominated exclusively by under-canopy originated individuals.

Through the analysis of abrupt growth changes we detected 226 maximum growth changes with an average value 4.7 ± 2.2 of growth pulse per tree. Growth pulses characterized by the maximum growth changes were scaled relative

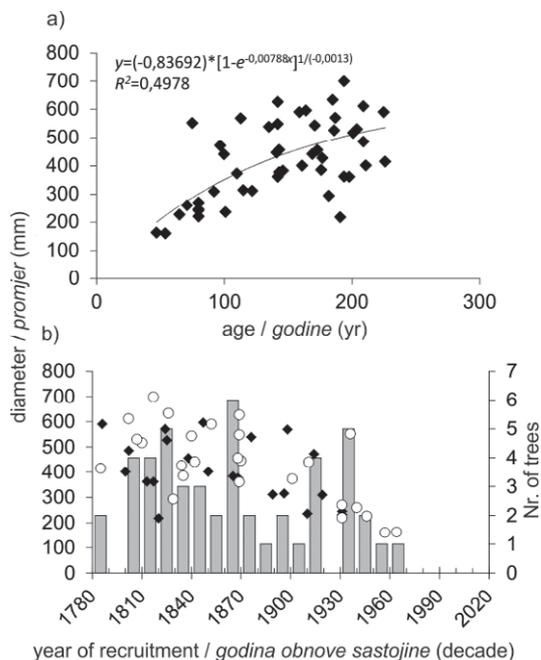


Figure 2. Age-diameter relationship of sampled trees. On the top, the data were fitted by Chapman-Richards growth curve. On the bottom, the years of recruitment (year of achieving the sampling height 0.5 m) are plotted with respect to the diameter of sampled trees. Black marker depicts the "gap originated" trees, white rings refer to "under canopy origin".

Slika 2. Odnos starosti i promjera uzorkovanih stabala. Gore, podaci su izravnati pomoću Chapman-Richards krivulje rasta. Dolje, godine obnove (godina postizanja visine od 0,5m) prikazane s obzirom na promjer uzorkovanih stabala. Crnim markerom obilježena su stabla nastala u progalama, bijeli krugovi odnose se na podrast.

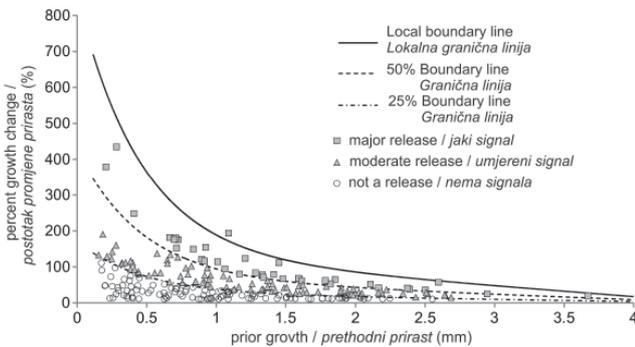


Figure 3. The maximum growth changes of each identified growth pulse plotted as a fraction of local *Picea abies* boundary line, the Low Tatras Mts., Slovakia.

Slika 3. Maksimalne promjene rasta svakog identificiranog signala natprosječnog debljinskog prirasta, kao dio lokalne granične linije smreke, Niske Tatre, Slovačka.

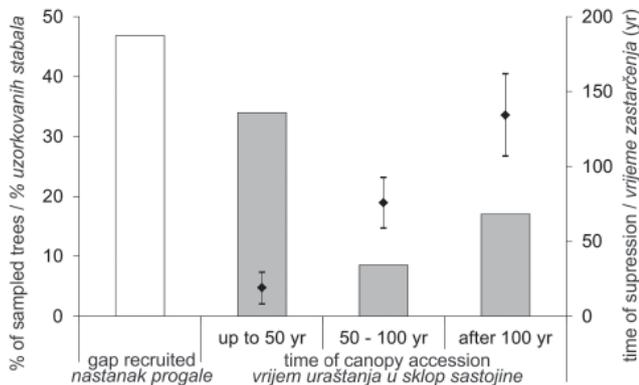


Figure 4. Age structure of sampled trees according to canopy accession date, Veľký Bok, Slovakia.

Slika 4. Dobna struktura uzorkovanih stabala prema vremenu uraštanja u sklop sastojine, Veľký Bok, Slovačka.

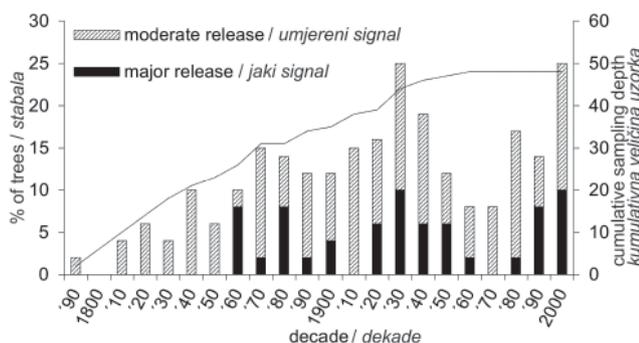


Figure 5. Temporal distribution of moderate and major releases of the investigated spruce dominated subalpine forest, the Low Tatras, Slovakia.

Slika 5. Vremenska distribucija umjerenih i jakih signala debljinskog prirasta istraživane pretplaninske sastojine obične smreke, Niske Tatre, Slovačka.

vely to developed boundary line (Fig.3). A total number of 124 growth pulses met the criterion "above the 20 % of the boundary line" and could be qualified as growth releases caused by canopy disturbance, 37 of these events were iden-

tified as a major release and 87 as a moderate intensity release. After the inspection of early growth rates we identified 22 sampled trees as the gap recruited (47 %). For the rest of individuals, we stated the canopy accession dates according to the occurrence and intensity of the first growth release. We paid special attention to the age when the tree entered the canopy. The analysis revealed that 34 % of trees reached the canopy position during the first 50 years of their live, almost 9 % entered the canopy in age from 50 to 100 years and 17 % of trees accessed the canopy after the 100 years of suppression (Fig.4).

The disturbance chronology is displayed in Figure 5. Disturbance events were recorded in every decade, however, we recognized three significant disturbance peaks during the inspected period. The first one occurred in 1860–1880, where the 18 % of trees showed major release and 21 % moderate release. Second period of disturbance activity occurs in 1920–1940 with the overall maximum in 1930. Major release was indicated for 10 % of trees, while 15 % of trees showed the moderate release. Third distinctive peak was recognized in 1980–2000 (Fig. 6).

Discussion Rasprava

The evaluation of age structure of cored trees revealed high age diversity of investigated forest. No remnants of understorey trees were observed during the sample collection in studied area. Therefore it is very likely the diameter and height structure of stand was distinctively uniform. Similar character of stand structure in this locality was described by Kucbel (2000a). Author stated the homogenized structure for six of total number of eight permanent research plots. Moreover, approximately 90 years ago, the stand characteristic written in forest management plan (1920–1930) described this locality as the open canopy homogenous mature spruce stands with rather high number of snags. Nagel et al. (2007) found the examination of forest developmental stages by means of the biometric measures of diameter and height as a quite difficult, because of a weak relationship between the real tree age and its diameter. Our finding can only confirm this statement ("diameter – age" relationship $R^2=0.49$).

High age variability points on the continuous tree regeneration. Evaluation of recruitment dates shows three distinctive waves of tree recruitment in 1800–1830, 1860 and 1910–1930.

Almost 50 % of inspected trees showed the early growth patterns referring to the open area growth. For the analysis we used the threshold value suggested by Svoboda et al. (2012). In our opinion, the number of trees that met the "gap recruited" criterion in the Veľký Bok site is underesti-

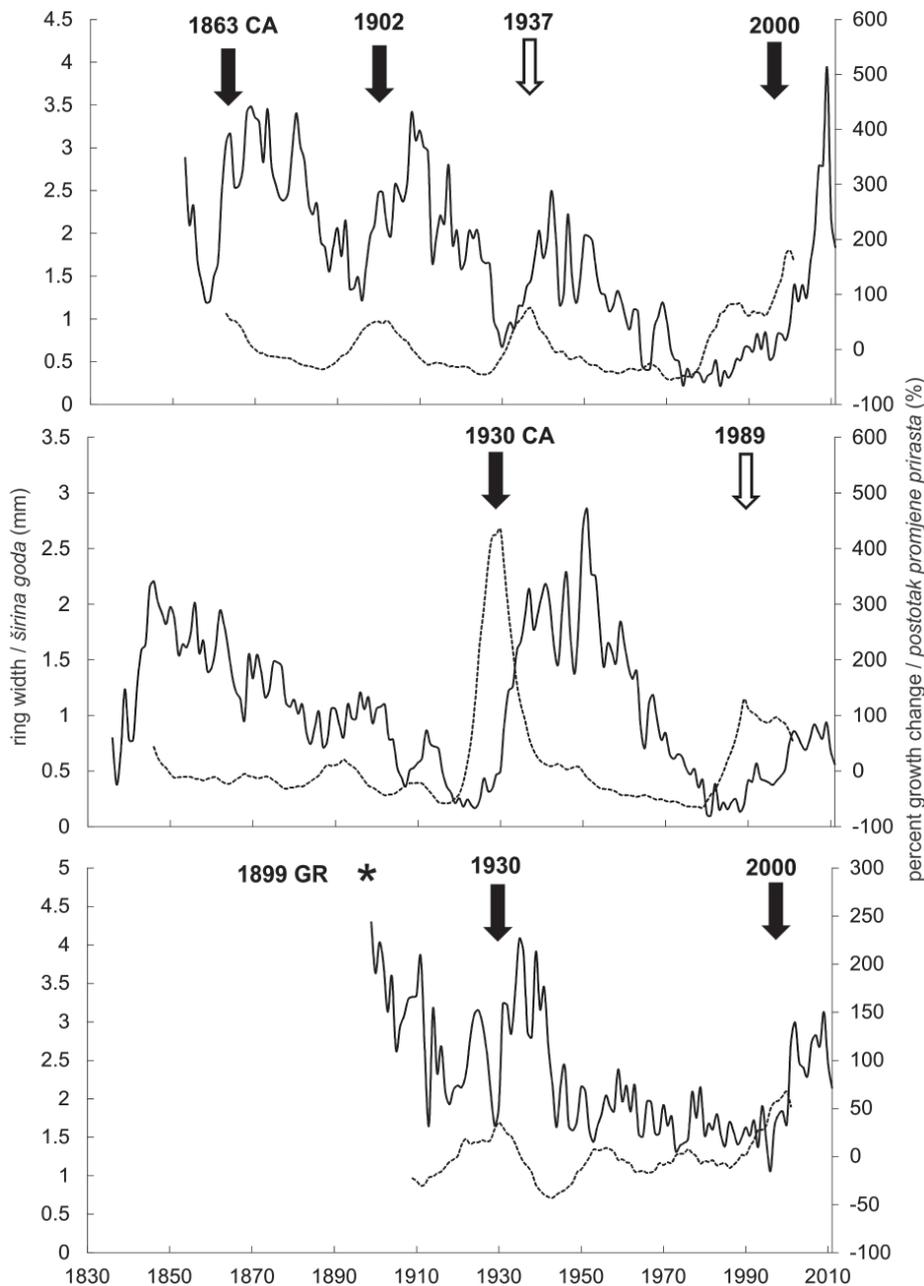


Figure 6. The example of individual response of trees to the same disturbance events. Top – Under canopy regenerated tree with canopy accession during the juvenile live stage. Middle – tree entered canopy after the removal of overtopping individual. Bottom – gap regenerated tree with two major releases. The ring width sequence (solid line) in relation to percent growth changes (dashed line). Black arrow designates the major release, white arrow marks moderate release, CA – canopy accession, GR – gap regenerated.

Slika 6. Primjer individualne reakcije stabala na isti poremećaj. Gore – Stablo obnovljeno pod zastorom krošanja s uraštanjem u sastojinski sklop tijekom juvenilnog stadija razvoja. Sredina – stablo je uraslo u sklop nakon što su odumrle previsoke jedinke. Dolje – stablo obnovljeno u progali s dva veća signala debljinskog prirasta. Slijed širine goda (puna crta) u odnosu na postotne promjene rasta (isprekidana crta). Crna strelica označava jači signal uslijed većih poremećaja, bijela strelica označava umjeren signal, CA – uraštanje u sklop, GR – obnova u progali.

mated, presumably due to more suitable growth conditions in NP Šumava (lower altitude, more oceanic climate, deeper soil). That's why the number of gap recruited trees has to be considered as a minimal recorded value. Further analysis is necessary for more accurate estimation, because it is not clear if the tree growing in harsh environment reacts on the increased light income by higher radial increment than the sapling growing under more suitable conditions. We expect the share of gap recruited trees of approximately 70 % as reported by Svoboda et al. (2012) from Šumava. As the spruce growing in higher altitudes needs more light income for sufficient regeneration (Holeksa 2001), the recruitment waves should be, as a rule, connected with the removal of overstory individuals.

Analysis of height shifts revealed that almost 34 % of individuals established under canopy reached canopy position during the first 50 years of their life, while more than 17 % of trees reached the canopy after the 100 years of suppression. Despite the increased light requirements of trees growing in harsh environment, spruce is able to regenerate under the closed canopy (e.g. on the logs) and wait for several decades till the overstory is opened (Leibundgut 1993; Kucbel 2011). Such structure creates a structural basis for the silvicultural concept of so-called mountain selection forest (Korpeř, Saniga 1995; Schütz 2011). This fact suggests that beside the large-scale wind disturbance, the development of spruce forest is affected by small-scale local disturbances or individual dieback of canopy trees due to bark

beetle outbreaks. Windstorms followed by bark beetle outbreaks lasting for several decades, so called the spruce phenomenon, are well known in conditions of spruce dominated forests (Okland; Bjornstad 2006; Lausch et al 2011).

Based on the analysis of growth sequences we can state that moderate to major wind events affected the surveyed subalpine spruce forest almost constantly over the last two centuries. Reconstruction of disturbance regime revealed three periods of growth releases during the last 150 years. This suggests that moderate to high intensity disturbance events occur rather periodically every 70 years and the growth pulses spanned for several decades. The first period of release events spanned from 1860 to 1890. When we considered the maximum growth response as the date when the event occurs, we can confirm the temporal position of disturbance events by examination of written historical sources. Our results are comparable with disturbance chronology constructed by Zielonka et al. (2011) for the High Tatras, because of the vicinity of these two sites (approx. 50 km). The first major event (1860) was also recorded by Zielonka et al. (2011) but authors were not able to find any historical record confirming the windstorm in this locality. However, the study of Zúbrik (2013) presents the high severity windstorm in the Low Tatras in 1870. Author notes that more than 6 million m³ of wood were downed by the wind during this event. The second period of disturbances in 1920–1940 has been documented by Zielonka et al. (2011). Author revealed the set of disturbance events in 1915, 1919 and 1941. Our results refer to the same sequence but we recorded a high severity event in 1931, what is consequently confirmed by Zúbrik (2013). Author presents the series of windstorms in 1921, 1925 and 1930. The sequence of wind disturbances, especially the event in 1930 was proven by historical record in forest management plan for the years 1920–1930. This series of windstorms are well documented by exact volumes of uprooted trees and reforestation goals. The volume of downed wood in affected management units increased during the windstorm period almost threefold. The third period shows the tight linkage with the broadly documented dieback of subalpine spruce forests due to emissions and acid rains during the 1990s.

The analysis of growth changes and tree recruitment clearly showed that the wind disturbances occurred periodically in the last 150 years. The recruitment evaluation confirmed that the disturbance regime of subalpine spruce forest is driven by the combination of gap and patch dynamics. For this reason, the recent state of studied spruce subalpine forest is probably only the natural stage of the spruce forest development. However, the lack of silvicultural intervention connected with global climate change contributes significantly to the current condition of subalpine forests. That's why the increased attention of forest ecologists and foresters should result in ecologically based, systematic management

of mentioned ecosystems. The silvicultural management should secure the sustainable presence and functioning of diversified forest stand. Special attention has to be paid to preservation of non-productive functions (Saniga 1997; Gubka 1998; 2000; Kucbel 2000a).

Conclusions

Zaključci

According to analysis of tree ages, type of recruitment as well as the reaction of sampled trees on the canopy opening we can state that researched subalpine spruce forest was affected by combination of large scale and small scale disturbances. The occurrence of large scale high severity events was proved almost periodically in the analyzed period while the intensive growth reaction of survived trees spanned for more than one decade.

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Sažetak

U radu se istražuje sastojinska dinamika pretplaninske šume obične smreke u Niskim Tatrama u Slovačkoj. U posljednje je vrijeme stanje planinskih šuma smreke nezadovoljavajuće, a posljedica je to jakih olujnih vjetrova i napada potkornjaka. Istraživanje se ponajprije bavi rekonstrukcijom prirodnih poremećaja koji su utjecali na lokalitet. Istraživanje je provedeno na reprezentativnom lokalitetu na području planine Velký Bok u Niskim Tatrama, središnja Slovačka. Nakon sječe sušaca, iz panjeva stabala smreke uzeli smo izvrtke (N=60). Koristili smo kriterij granične linije za procjenu pojave signala natprosječnog debljinskog prirasta.

Rekonstruirali smo kronologiju lokalnih poremećaja i obnove sastojine. Jasno su se pokazale tri iznadprosječne kulminacije debljinskoga prirasta, u razdoblju do 1860–1880.; 1920–1940. i 1980–2000. godine. Istraživanjem povijesnih izvora potvrdili smo uočena razdoblja prirodnih poremećaja. Što se tiče obnove sastojine, 50 % anal-iziranih stabala zadovoljili su kriterij obnovljenih progala. Vremenski položaj prirodne obnove sastojine usko je povezan s pojavom jakih prirodnih poremećaja. Dobiveni rezultati ukazuju na činjenicu da su jaki vjetrovi prirodna pojava u pretplaninskim šumama smreke te da je ukupna tekstura istraživanih šuma posljedica djelovanja uzajamne kombinacije dinamike manjih i većih progala.

KLJUČNE RIJEČI: natprosječni debljinski prirast, obična smreka, granična linija, Središnja Europa, prirodni poremećaji