Silva Gabreta	vol. 26	p. 65–79	Vimperk, 2020

The structure of natural regeneration in a mountain spruce forest 5 years after parent stand dieback

Jaroslav Červenka[1,2,*], Radek Bače[2], Jitka Zenáhlíková[1] & Miroslav Svoboda[2]

[1] *Šumava National Park, 1. máje 260, CZ-385 01, Vimperk, Czech Republic*
[2] *Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 1176, CZ-16521 Prague, Czech Republic*
[*] jaroslav.cervenka@npsumava.cz

Abstract
The tree natural regeneration and seed bank that survives a large-scale stand-replacing disturbance fully determines the future forest structure until new generation trees reach seed maturity and the supply of seeds is restored. We asked the following questions: (*i*) Does the advance regeneration stage prevail in the stand? (*ii*) Does the tree species composition changed after disturbance? (*iii*) Does the regeneration height structure change depend on elevation and characteristics of the previous stand? Mean seedlings (<130 cm) density was 4000 individuals per hectare 5 years after the disturbance; rowan covered 2% of the regeneration. The density of saplings (≥130 cm) was 252 individuals per hectare, of which 19% were rowan individuals. The advance regeneration consisted of 88% of all individuals. Microsites mostly preferred were soil covered by mosses (32% of individuals), the tree base of living mature trees and snags (28% of individuals), and dead wood (27% of individuals). The density of saplings significantly decreased with increasing elevation; for seedlings, this trend was not significant. Even an elevation gradient of 100 m can have a major impact on the growth rate of the regeneration. Although the variability of stand characteristics was high, no significant effect was recorded for any of the height categories of spruce and rowan with regard to the density of the regenerated stand. Our results provide the example of stands, where structure of regeneration after the disturbance is not explained by previous stand characteristic. Lower saplings density in higher elevation is probably caused by limiting growth conditions such a cold. High heterogeneity of regeneration structure must depend on many other factors.

Key words: Norway spruce, advance regeneration, elevation, bark beetle disturbance, Šumava NP

Introduction

Disturbances form an integral part of the dynamics in many ecosystems around the world (e.g. Bouget & Duelli 2004, Kulakowski & Bebi 2004, McDowell et al. 2020). In the Central Europe, disturbances caused by winds are the most common type of disturbance; for spruce stands, bark beetle outbreak (*Ips typographus* L.) is particularly the case (Kulakowski & Bebi 2004). In recent decades, disturbances have increased in terms of numbers and intensity (Lausch et al. 2011). The warmer climate causes physiological stress on trees and accelerates the bark beetle development (Raffa &Aukema 2008, Seidl et al. 2014). Consequently, rising intensity of disturbance can be expected as the climate change increases (Seidl et al. 2014, Dobor et al. 2020). The aftermath left by any disturbance is referred to as biological legacy

(Čada et al. 2013, Frelich et al. 2018); it may involve stand structure that has been preserved from the previous stand, the amount of dead wood, or advance regeneration.

A bark beetle disturbance delivers completely different conditions for natural regeneration than fire or wind. The key differences can be seen in the fact that stands do not die at once; rather, the process takes several years (Sproull et al. 2015, Červenka et al. 2016). The stand microclimate also changes gradually as the parent stand dieback (Jonášová & Prach 2004, Metslaid et al. 2007). In the case of disturbance caused by bark beetles, there is no disruption of the soil, the vegetation cover and the advance regeneration (Storanet & Rolstad 2004). Advance regeneration and its structure, both are the natural legacy that drives the process of natural regeneration in such ecosystems (Svoboda et al. 2010) and they are linked to the previous stand (Wild et al. 2014, Bače et al. 2015). The process of mountain spruce forests regeneration after bark beetle outbreak has already been described to some extent (Holeksa et al. 2007, Zeppenfeld et al. 2015), but it is really different with regard to the other types of disturbances. Therefor is impossible to apply knowledge sourced from reports studying other types of disturbances (Gromstev 2002, Goetz et al. 2007) or from forest stands with a more homogeneous structure found for example in Scandinavia (Angelstam & Kuuluvainen 2004), to Central European mountain spruce forest stands affected by bark beetle gradation.

The management and the future appearance of this stands is still hot topic, whether it involves protected areas or commercial forests. Knowing the amount of natural regeneration and how the process works is a key factor in making management decisions. Presence of regeneration after the stand-replacing disturbance determines the future appearance and development of these ecosystems (Svoboda et al. 2010). Accordingly, understanding the process of stand replacement after the parent stand dieback is a major challenge. So far, we have little knowledge about the impact of the initial stand structure or the elevation on the condition of the newly emerging stand or the advance regeneration. Current scientific papers are not consistent in how large the proportion of the advance regeneration is compared to disturbance-related or post-disturbance regeneration. Some studies argue that disturbance related or the post-disturbance seedlings constitute just a relatively small portion of the all regeneration (Svoboda et al. 2010, Nováková et al. 2015). On the contrary, other studies have found that disturbance-related regeneration may represent the bulk of the new forest stand (Wild et al. 2014, Macek et al. 2016). Most studies also focus on regeneration from a certain height (Zeppenfeld et al. 2015). We monitored all individuals found in the stand independently of the height, immediately after a disturbance caused by bark beetles. The present paper specifically answers the following questions: (*i*) Does the advance regeneration stage prevail in the stand? (*ii*) Does the tree species composition change after the disturbance? (*iii*) Does the regeneration height structure change depend on elevation and characteristics of the previous stand?

Materials and methods

Location

This study comes from a region of mountain spruce forests found in Šumava National Park (NP). The area of interest is called Trojmezná, and is situated in a territory found between the mountain tops of Třístoličník and Trojmezná and stretching along the border with Germany.

The area of 599 ha was managed as a "national nature reserve" from 1933 until it was included, with the foundation of the NP, in what is now Conservation Zone 1 (Fig. 1). The altitude range of whole Zone 1 is 945–1378 m a.s.l. It is one of the best preserved complexes of mountain spruce forests in the Czech Republic (CR) without any major influence of human (Svoboda et al. 2010, Červenka et al. 2016). In the last 300 years, the structure and the nature of the local stands both were shaped by a mode of less frequent, medium-intensity disturbances, i.e., those removing less than 50% of co-dominant trees (Janda et al. 2014). Very recently, an outbreak of bark beetle caused 100% parent stand mortality in 2008 (Svoboda et al. 2010). The stands had already been disrupted, to some extent, by barkbeetle (*Ips typographus* L.) at the beginning of the present century; subsequently, the devastating Hurricane Kyrill swept across the NP territory in 2007 to start barkbeetle outbreaks which affected the entire area of interest by 2010 (Červenka et al. 2016). Affected stands in this area were left to spontaneous development, giving us the opportunity to study the natural regeneration after a bark beetle disturbance.

In 2001, three elevation transects were established on a moderate northern slope with an inclination of 8° (Svoboda 2005). Transects consist of a total of 18 circular plots (3 complexes of 6 plots; 0.2 hectares per plot; r = 25.23 m). The plot elevation ranged from 1 220 to 1 340 m. The distance between elevation transects is approx. 500 m; the spacing of the plot centres

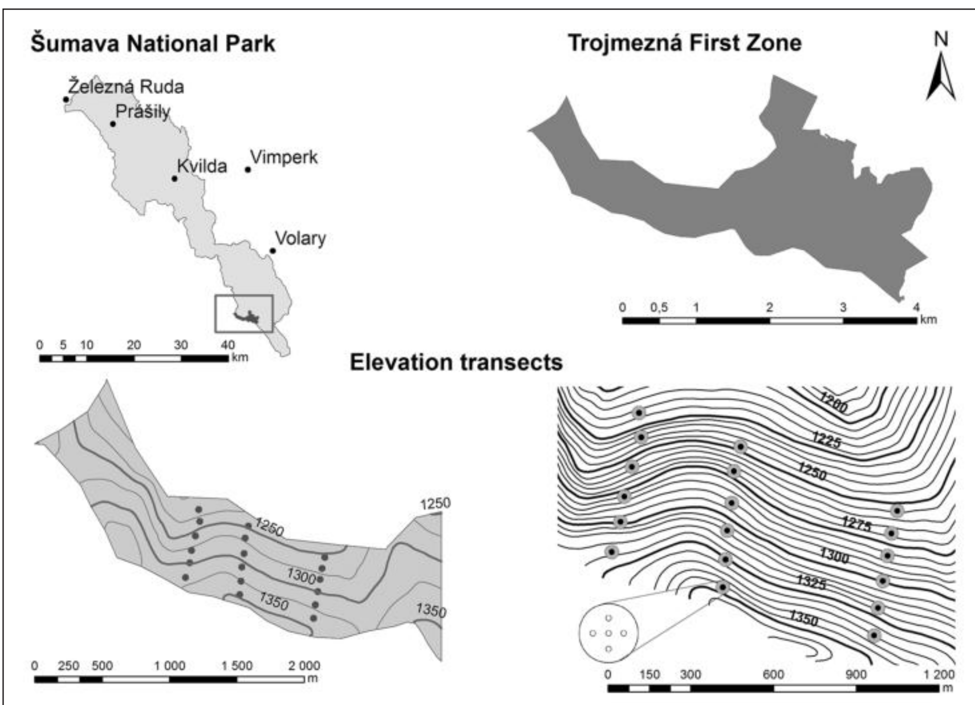

Fig. 1. Schema of Šumava NP (upper left-hand corner) with locality Trojmezná (upper right-hand corner). In lower part is shown 18 permanent research plots (distance between transects is approx. 500 m, distance between plots through transect is 100 m).

within the transect axis is 100 m vertically (Fig. 1). Annual precipitation is about 1 400 mm locally; average annual temperature is around 4°C. Plant communities are classified as *Athyrio alpestris-Piceetum* (Neuhäuslová et al. 1998).

Data collection

The exact positions of tree individuals that reached a minimum height of 1.3 m till maximal DBH 69 mm ("saplings") were measured using the Field-Map technology (IFER-MMS 2016, http://www.fieldmap.cz) in year 2012. Natural regeneration microsite was identified for each individual. The inventory of regeneration of less than 1.3 cm height ("seedlings") was carried out on 5 smaller circular plots (25 m^2; r = 2.82 m), established on each of the 18 plots. One of those 5 plots had its centre identical to that of the plot already set out, while each of the other 4 plots had its centre 10 m from the centre of the plot already set out, each time toward one of the cardinal directions (N, S, E, and W; the distances were measured using Haglöf Vertex III Hypsometer (height resolution: 0.1 m; distance resolution: 0.01 m). The cardinal directions were determined using the Field-Map technology. For each of the regenerated areas, the species was determined while recording the number, the precise height, and the microsite. The microsite was defined based on the dominant species of vegetation or cover occurring in the immediate vicinity of the each individual. The following microsites were determined: tree litter, a log, stump, a windfall, a tree foot and soil with vegetation – the last mentioned microsite was subdivided into the categories of soil with mosses, herbs and ferns. For dead wood, five degrees of decay were differentiated using an iron spike (20 cm long, 7 mm in diameter) (Sippola & Renvall 1999).

Data processing

The natural spruce regeneration was grouped into the two categories: (1) advance regeneration – trees established prior to the outbreak and (2) post-disturbance regeneration – trees established after canopy dieback. To classify the naturally regenerated stand as advance regeneration or post-disturbance individuals of spruce, we used a specific relationship between the height and the age of the regenerated trees. The age was determined by counting annual whorls and bud scars of the individuals (Niklasson 2002), which is reliable for young spruce saplings (Zielonka 2006, Bače et al. 2011). We are aware that this method could misclassify some individuals, but we choose this method as the best possible option. Out of more than 6 000 regenerated individuals permanently monitored, the average height for 5 years old individuals was determined (5 years = period between the time the disturbance started and the time when data were collected). Obtained value of 10.2 cm (SD = 4.04 cm) was then used as a threshold for determining the proportion of the advance regeneration and post-disturbance regeneration. For this height were numbers of advance regeneration classified as post-disturbance and conversely in balance. A paired-samples sign test was used to verify the hypothesis of dominance of the advance regeneration.

We also tested the dependence of the number of regeneration (both spruce and rowan trees) on stand characteristics and on the elevation. The stand characteristics were represented by mean DBH, number of trees, the basal area and the canopy cover. Stand characteristics (Table 1) were taken from a paper by Červenka et al. (2016). The testing was carried out using

Table 1. Stand characteristics before disturbance measured in 2001 (DBH, number of trees, basal area, crown area) and altitude for each permanent plot.

Plot no.	DBH (cm)	SD	No. of trees (pc/ha)	Basal area (m^2/ha)	Crown area (m^2/ha)	Altitude (m a.s.l.)
1	53.1	24.3	215	61.1	2812.1	1250
2	51.3	14.1	300	66.6	2964.0	1270
3	49.3	16.7	300	59.5	1820.3	1285
4	41.0	11.6	415	55.3	3130.6	1300
5	40.0	12.7	405	57.9	2891.9	1320
6	32.8	11.7	625	53.7	3841.2	1335
7	43.9	18.9	280	50.2	1268.1	1245
8	53.9	20.9	195	54.0	1764.4	1270
9	47.5	18.3	280	54.5	2755.3	1290
10	45.2	14.9	385	64.7	4271.5	1315
11	38.9	13.1	530	66.6	5127.9	1330
12	35.6	10.4	585	58.2	3738.4	1350
13	47.2	29.8	150	40.7	2392.7	1220
14	60.4	16.4	205	63.8	2405.1	1235
15	55.6	13.0	225	59.4	694.0	1260
16	48.4	18.1	270	52.1	1570.9	1280
17	43.5	16.8	290	48.0	2733.1	1305
18	37.1	12.3	475	57.1	3764.7	1320
Mean	45.8	–	341	56.9	2774.8	1288
SD	7.2	–	135.3	6.5	1087.0	36

generalized linear models (GLMs) with negative binomial distribution respecting the data distribution with the pre-dominance of low values with a little frequency of extremely high values. As a priority, we used the variation of inflation factors (VIF) to verify the co-linearity of the potential explanatory variables (Mansfield & Helms 1982). The VIF value was calculated using the R^2 value of the linear regression of this variable (left side) for each of the explanatory variables and opposed to all the remaining explanatory variables (right side):

$$VIF_j = \frac{1}{1-R_j^2}$$

Each of the explanatory variables with a VIF value greater than 5 was gradually deleted (VIF values were again recalculated after deleting of one variable). On this basis, explanatory variables were identified which have not been significantly correlated with the other explanatory variables. These independent variables were subsequently tested using negative binomial regression models. The individual candidate negative binomial regression models were compared by the Chi-test using backward selection. The statistical significance of

Table 2. Average height of regeneration for both species in different height categories.

Species	Height category (cm)	Median of height (cm)	Average of height (cm)	SD
Norway spruce	0–1.3	27	36	28
	≥1.3	165	183	57
Rowan	0–1.3	83	75	34
	≥1.3	162	186	69
All	0–1.3	28	37	29
	≥1.3	165	183	165

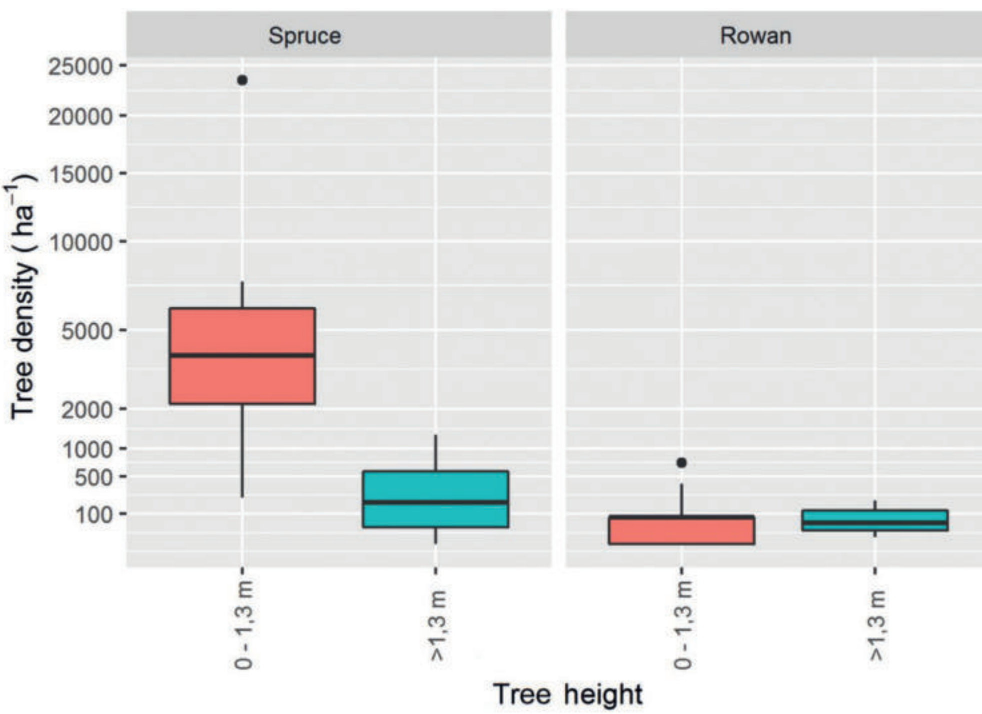

Fig. 2. Density of spruce and rowan regeneration for each height categories (0–1.3 m resp. ≥1.3 m). Box plots represent median, quartile and range of data

the final models was verified by Pearson's chi-squared testing using the Chi-squared test, residual deviance and degrees of freedom. Calculations were performed using R software (R Core Team 2018).

Results

Natural regeneration structure

Immediately after a large-scale disturbance, regeneration of only two tree species was recorded on the plots – Norway spruce (*Picea abies*) and rowan (*Sorbus aucuparia*). For either of the species, the number of seedlings (<130 cm) and saplings (≥130 cm) was highly variable comparing the plots subjected to the research (Fig. 2). The values of seedlings ranged from 240 to 23 520 individuals per hectare, with median 4 000 trees per hectare. Spruces accounted for 98% of the regeneration found, rowan for 2%. For saplings, a minimal found number was 5 individuals per hectare while the maximal observed number was 1 430 individuals per hectare. The median of saplings density was 252 trees per hectare, involving a higher proportion of rowan trees (19%).

The average height of seedlings and saplings was 37 cm (±29 SD) and 183 cm (±59 SD), respectively. For the average height of regeneration for each species and height category, see Table 2. For spruce, the advance regeneration stage prevailed in the stands ($N = 18$, $p<0.01$), accounting for a total of 88%; the percentage of advance regeneration ranged between 68% and 100% on the individual plots.

Microsites

The most preferred microsites for spruce regeneration are soil covered by mosses (32% of individuals), tree base of living mature trees and snags (28% of individuals) and dead wood (27% of individuals). Seedlings were found only on the dead wood which was already present before the disturbance (from decay stage III). Grasses, ferns and herbs, which covered the largest rate of the plots, were occupied to the least extent (8%), similarly the litter (5%).

The effect of the stand characteristics and elevation on the amount of regeneration

Although the variability of the stand characteristics was high in the study area (Table 1), no effect was demonstrated of any of the stand characteristics monitored by us for the seedlings of spruce. The density of seedlings did not change even with elevation. For rowan seedlings, testing the amount against explanatory variables was not possible due to the small number of individuals on each of the plots.

For saplings, only elevation had a significant effect on the density of spruce and rowan individuals, as the only one out of the explanatory variables ($P<0.0001$). The variability explained by elevation was 40% resp. 37% for spruce and rowan. The relationship between the amount of regeneration and elevation is shown in Fig. 3. As the elevation rises, there is much more regeneration with homogeneous heights; the height of individuals is generally lower. The most of saplings (90%) were found in the lower elevation half of the study area (Fig. 4). This resulted in a fact that in the lower elevation half of the study area we can find more heterogeneous stands rather than in the higher elevation portions (Fig. 5). No effect of elevation on advance regeneration density was demonstrated. Despite Fig. 6 shows a slightly declining (not significant) trend.

Discussion

The natural regeneration occurring in stands following large-scale disturbances determines the future appearance of these forests; any failure of such processes could have a long-term effect on the whole ecosystem (Grassi et al. 2004). In many cases, disturbances support an increase in numbers of the pioneer species, thereby increasing the biodiversity of the disturbed stand for a certain period of time (Kuuluvainen & Aakala 2011). In our case, i.e., in the setting of a Central European mountain spruce forest, the species composition remained the same as that of the parent stand (Heurich 2009, Zeppenfeld et al. 2015). The dominant species is again spruce with small proportion of rowan. By skipping the pioneer stage of regeneration, the classical theory of forest development after a large-scale disturbance, as described by Korpel (1995) is denied. In our case the species composition does not change. Mountain spruce forest stands are generally recovered through spruce once again immediately after bark beetle large-scale disturbance. Rowan was represented to a minor extent. This was particularly

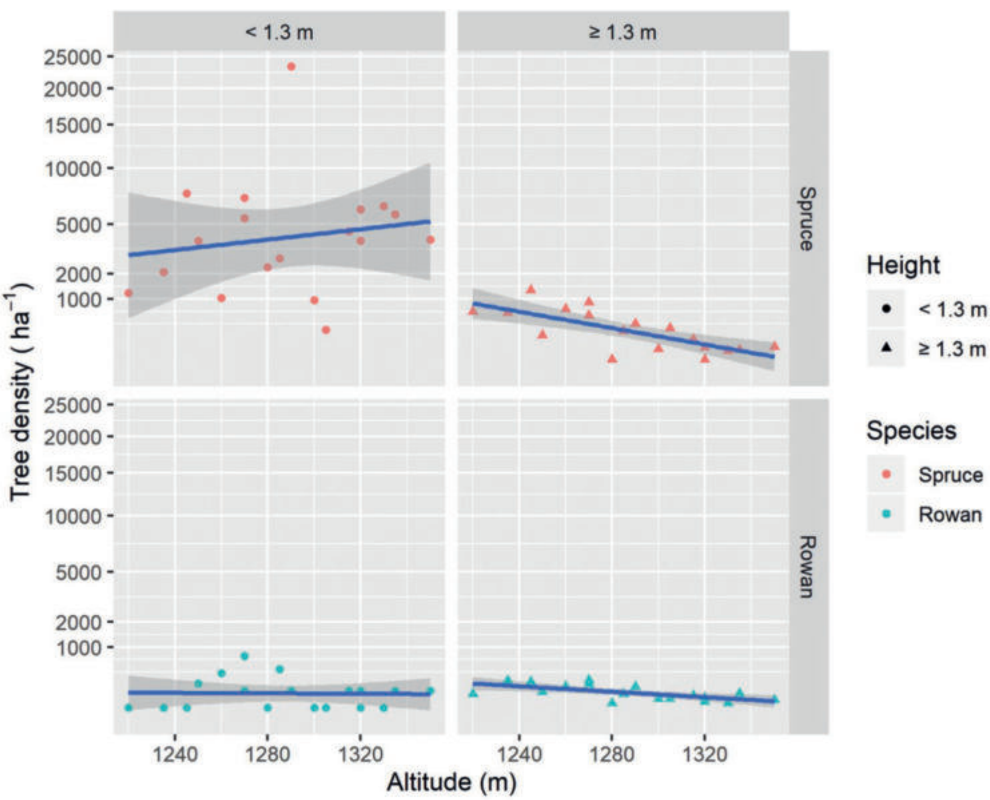

Fig. 3. Spruce and rowan density in different altitude.

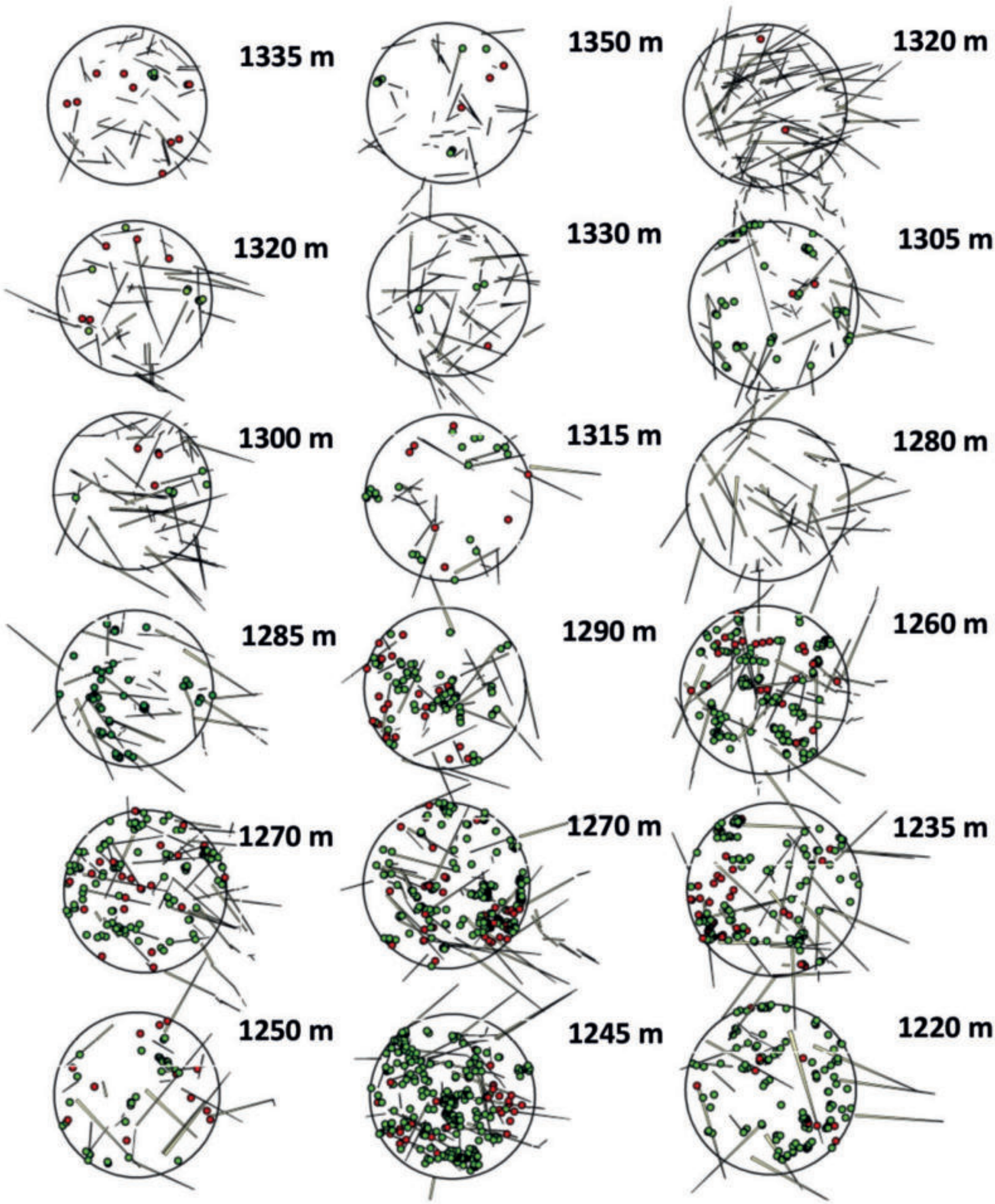

Fig. 4. The map of distribution of fallen logs and natural regeneration (≥1.3 m) in area of interest. Green colour marks the spruce regeneration, red colour shows regeneration of rowan. Altitude ranges from 1220 m a.s.l. (bottom of the picture) till 1340 m a.s.l.

true for the seedlings, which is consistent with studies from sub-alpine forest regions (MERGANIČ et al. 2003, JONÁŠOVÁ & PRACH 2004, ZENÁHLÍKOVÁ et al. 2011, NOVÁKOVÁ & EDWARDS-JONÁŠOVÁ 2015). The proportion of rowan saplings was relatively high (19%). In mountain areas is rowan dependent on the establishment of a sufficient number of individuals before canopy opening of the parent stand (ŻYWIEC & LEDWOŃ 2008). As a result, the species is gaining a height advantage, making it competitive over the herbaceous vegetation (FISCHER et al. 2002). The tree alone is also able to react significantly to supply of light through increased increment, which explains its greater presence in the saplings category. No pioneer tree species were recorded in the stands. These tree species are comfortable with cases of soil disruption which are not so frequent in the event of disturbances due to bark beetles (HEURICH 2009). Only a small amount of the area under monitoring was affected by windfalls (ČERVENKA et al. 2016), which may be the cause of the absence of pioneer species.

The amount of seedlings (1.3 m or below) we found (4 000 individuals per hectare) is not considerably inconsistent with values described in studies from similar locations (HEURICH 2009, ČÍŽKOVA et al. 2011, ZENÁHLÍKOVÁ et al. 2011). For successful renewal of such stands, not only numbers, but also distribution of height is important. The greatest mortality is reported for the smallest individuals (JONÁŠOVÁ & PRACH 2004, ZENÁHLÍKOVÁ et al. 2011, ČERVENKA et al. 2014), increasing height also rises the rate of survival. MACEK et al. (2016) reports a mortality rate of 5% for individuals above 0.5 m; in our case, the regeneration rate is nearly 30% for

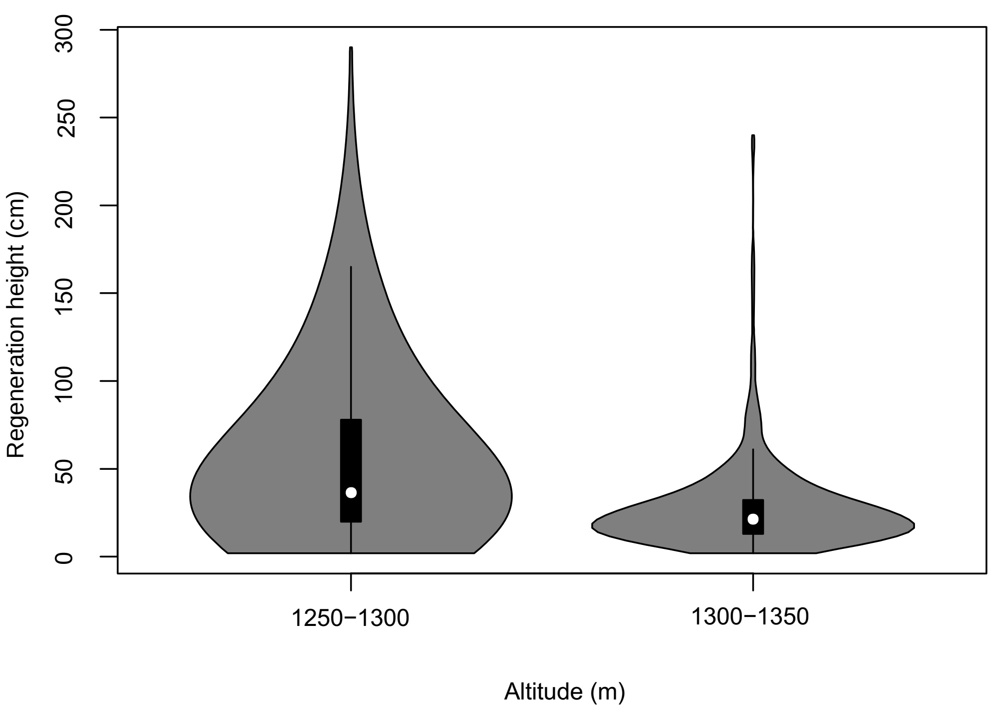

Fig. 5. Height of regeneration in different altitudes (1250–1300 m a.s.l.; 1300–1350 m a.s.l.). Violin plots represent median, quartiles, range without outliers and kernel density of regeneration

this height category. The density of individuals we have found ensure a sufficient regeneration of these stands.

Some studies indicate a decrease in the density of regeneration with increasing elevation (Vorčák et al. 2006, Konôpka et al. 2019). In our case, we did not see a decrease in the amount within a height gradient of 100 m, but with increasing elevation we saw differences in the height distribution of the natural regeneration. Five years since the disturbance started, we observed the absence of saplings at higher elevations in contrast with lower zones where their numbers were sufficient. Even such a short height gradient has a major impact on the rate of regeneration growth. As the elevation of the regeneration increases, a higher amount of light is needed for the vegetation's growth (Pisek & Winkler 1959). There are worse weather conditions at higher elevations that affect growth and mortality of the regeneration (Rammig et al. 2006). These may be factors that explain the lower amount of regeneration in such zones. After the dieback of parent stand there may be a gradual increase in mortality of regeneration (Macek et al. 2016) and also increase in variability of regeneration density may occur with rising elevation (Vorčák et al. 2006, Konôpka et al. 2019). Within a maximum of four years after the dieback of parent stand, effect of opening has not yet been demonstrated in our case; probably, the period of time is too short for the effect of a strong disturbance to be manifest (Červenka et al. 2014).

According to some authors (e.g. Holeksa et al. 2007), the spatial structure of the stands

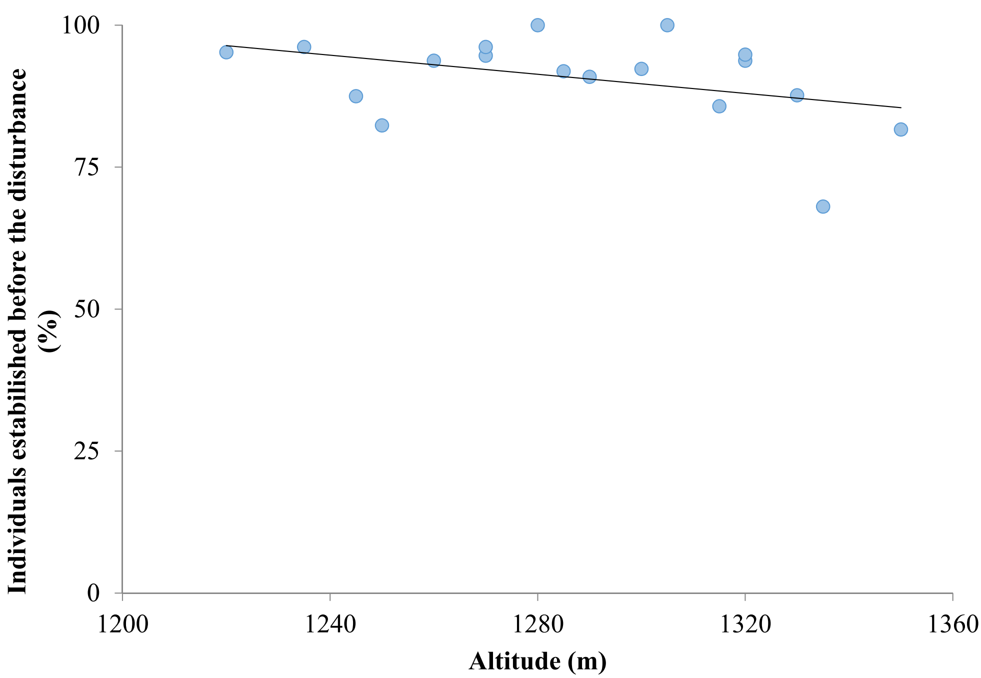

Fig. 6. Proportion of advance regeneration in different altitude.

has an impact on the amount of regeneration. Despite the fact that the stand characteristics were very variable when comparing our permanent plots, their effect was not significant for either of the tree species present. Some studies show that the post-disturbance regeneration structure can also be significantly influenced by the structure of the stand before the disturbance (Wild et al. 2014, Bače et al. 2015). The lower elevation as well as the upper elevation portion of our site, both were shaped by a different disturbance history (Svoboda et al. 2012). Unfortunately, any exact line of this difference cannot be defined precisely in the field (Svoboda et al. 2012) – it is a continuous transition. This did not allow the testing of this factor. However, it is possible that the more heterogeneous structure with more gaps in the lower section may have been reflected in the heterogeneity of regenerated stand, as other studies confirm (Wild et al. 2014, Bače et al. 2015). Regeneration in the lower portion can be assumed to respond quickly to the opening of the stand. In contrast, in the upper elevation part of the site with a lower density and height of the regeneration, the development will be slower, with higher mortality of regeneration. It can result in a wide age structure, similar to the former stand.

Conclusions

We monitored state of natural regeneration in Central European mountain spruce forest 5 years after a large-scale stand-replacing disturbance. The density of individuals we have found ensure a sufficient regeneration of these stands. In our case species composition remained the same as that of the parent stand before the disturbance. The dominant species is still spruce with small proportion of rowan. Most of the natural regeneration was established prior to complete dead of parent stands. The density of saplings (>1.3m) significantly decreased with increasing elevation. We proofed an elevation gradient of 100 m can have a major impact on the growth rate of the regeneration. We expected significant impact of the previous stand characteristics on density and height structure of regeneration, but no significant effect was recorded for any of the height categories of spruce and rowan.

Our plots (state of regeneration) will be re-measured again in 2021. It will be really interesting to see development of regeneration 15 years after canopy dieback of parent stand.

Acknowledgement. This study was supported by the Czech Science Foundation (project No. P503-19-16605S) and MSMT projects LTC17055 and LTT20016. Comments by anonymous reviewers have greatly improved the manuscript. We would like to thank M. Pospíšilová and M. Feriancová for the assistance during the field work.

References

Angelstam P. & Kuuluvainen T., 2004: Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. *Ecological Bulletins*, 51: 117–136.

Bače R., Svoboda M. & Janda P., 2011: Density and height structure of seedlings in subalpine spruce forests of Central Europe: logs vs. stumps as a favourable substrate. *Silva Fennica*, 45(5): 1065–1078.

Bače R., Svoboda M., Janda P., Morrissey R.C., Wild J., Clear J.L., Čada V., Donato D.C. & Chen H.Y.H., 2015: Legacy of pre-disturbance spatial pattern determines early structural diversity following severe disturbance in montane spruce forests. *PloS One*, 10(9): e0139214.

Bouget C. & Duelli P., 2004: The effects of windthrow on forest insect communities: a literature review. *Biological Conservation*, 118(3): 281–299.

Brang P., 1998: Early seedling establishment of *Picea abies* in small forest gaps in the Swiss Alps. *Canadian Journal of Forest Research*, 28(4): 626–639.

Čada V., Svoboda M. & Janda P., 2013: Dendrochronological reconstruction of the disturbance history and past development of the mountain Norway spruce in the Bohemian Forest, central Europe. *Forest Ecology and Management*, 295: 59–68.

Červenka J., Bače R. & Svoboda M., 2014: Stand-replacing disturbance does not directly alter the succession of Norway spruce regeneration on dead wood. *Journal of Forest Science*, 60(10): 417–424.

Červenka J., Bače R., Zenáhlíková J. & Svoboda M., 2016: Changes in stand structure, dead wood quantity and quality in mountain spruce forest after severe disturbance. *Reports of Forestry Research*, 61(4): 254–261.

Čížková P., Svoboda M. & Křenová Z., 2011: Natural regeneration of acidophilous spruce mountain forests in non-intervention management areas of the Šumava National Park – the first results of the Biomonitoring project. *Silva Gabreta*, 17: 19–35.

Dobor L., Hlásny T., Rammer W., Zimová S., Barka I. & Seidl R., 2020: Spatial configuration matters when removing windfelled trees to manage bark beetle disturbances in Central European forest landscapes. *Journal of Environmental Management*, 254: 109792.

Frelich L.E., Jõgiste K., Stanturf J.A., Parro K. & Baders E., 2018: Natural disturbances and forest management: interacting patterns on the landscape. In: *Ecosystem services from forest landscapes*. Perera A.H, Peterson U., Pastur G.M. & Iverson L.R. (eds) Springer, Cham, The Switzerland: 221–248.

Goetz S.J., Mack M.C., Gurney K.R., Randerson J.T., Houghton R.A., 2007: Ecosystem responses to recent climate change and fire disturbance at northern high latitudes: observations and model results contrasting northern Eurasia and North America. *Environmental Research Letters*, 2(4): 045031.

Grassi G., Minotta G., Tonon G. & Bagnaresi U., 2004: Dynamics of Norway spruce and silver fir natural regeneration in a mixed stand under uneven-aged management. *Canadian Journal of Forest Research*, 34(1): 141–149.

Gromtsev A., 2002: Natural disturbance dynamics in the boreal forests of European Russia: a review. *Silva Fennica*, 36(1): 41–55.

Heurich M., 2009: Progress of forest regeneration after a large-scale *Ips typographus* outbreak in the subalpine *Picea abies* forests of the Bavarian Forest National Park. *Silva Gabreta*, 15(1): 1–13.

Holeksa J., Saniga M., Szwagrzyk J., Dziedzic T., Ferenc S. & Wodka M., 2007: Altitudinal variability of stand structure and regeneration in the subalpine spruce forests of the Poľana biosphere reserve, Central Slovakia. *European Journal of Forest Research*, 126(2): 303–313.

Janda P., Svoboda M., Bače R., Čada V. & Peck J.E., 2014: Three hundred years of spatio-temporal development in a primary mountain Norway spruce stand in the Bohemian Forest, central Europe. *Forest Ecology and Management*, 330: 304–311.

Jonášová M. & Prach K., 2004: Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak. *Ecological Engineering*, 23(1): 15–27.

Konôpka B., Šebeň V. & Pajtík J., 2019: Species composition and carbon stock of tree cover at a postdisturbance area in Tatra National Park, Western Carpathians. *Mountain Research and Development*, 39(1): R71–R80.

Korpel Š., 1995: *Pralesy Slovenska* [*Primeval forests of Slovakia*]. Veda, Bratislava, 328 pp. (in Slovak).

Kulakowski D. & Bebi P., 2004: Range of variability of unmanaged subalpine forests. *Forum für Wissen*, 47–54.

Kuuluvainen T. & Aakala T., 2011: Natural forest dynamics in boreal Fennoscandia: a review and classification. *Silva Fennica*, 45(5): 823–841.

Lausch A., Fahse L. & Heurich M., 2011: Factors affecting the spatio-temporal dispersion of *Ips typographus* (L.) in Bavarian Forest National Park: A long-term quantitative landscape-level analysis. *Forest Ecology and Management*, 261(2): 233–245.

Macek M., Wild J., Kopecký M., Červenka J., Svoboda M., Zenáhlíková J., Brůna J., Mosandl R. & Fisher A., 2017: Life and death of *Picea abies* regeneration after stand-replacing bark-beetle outbreaks. *Ecological applications*, 27(1): 156–167.

MANSFIELD E.R. & HELMS B.P., 1982: Detecting multicollinearity. *The American Statistician*, 36(3a): 158–160.

MCDOWELL N.G., ALLEN C.D., ANDERSON-TEIXEIRA K., AUKEMA B.H., BOND-LAMBERTY B., CHINI L. & HURTT G.C., 2020: Pervasive shifts in forest dynamics in a changing world. *Science,* 368: 6494.

MERGANIČ J., VORČÁK J., MERGANIČOVÁ K., ĎURSKÝ J., MIKOVÁ A., ŠKVARENINA J., TUČEK J. & MINDÁŠ J., 2003: Monitoring diverzity horských lesov severnej Oravy [Monitoring of diversity of mountain forests of north Orava]. EFRA, Tvrdošín, 200 pp. (in Slovak).

METSLAID M., JOGISTE K., NIKINMAA E., MOSER W.K. & PORCAR-CASTELL A., 2007: Tree variables related to growth response and acclimation of advance regeneration of Norway spruce and other coniferous species after release. *Forest Ecology and Management*, 250: 56–63.

NEUHÄUSLOVÁ Z., BLAŽKOVÁ D., GRULICH V., HUSOVÁ M., CHYTRÝ M., JENÍK J., JIRÁSEK J., KOLBEK J., KROPÁČ Z., LOŽEK V., MORAVEC J., PRACH K., RYBNÍČEK K., RYBNÍČKOVÁ E. & SÁDLO J., 1998: Mapa potenciální přirozené vegetace České republiky, textová část [Map of potential natural vegetation of the Czech Republic, explanatory text]. Academia, Praha, 341 pp. (in Czech).

NIKLASSON M., 2002: A comparison of three age determination methods for suppressed Norway spruce: implications for age structure analysis. *Forest Ecology and Management*, 161: 279–288.

NOVÁKOVÁ M.H. & EDWARDS-JONÁŠOVÁ M., 2015: Restoration of central-European mountain Norway spruce forest 15 years after natural and anthropogenic disturbance. *Forest Ecology and Management*, 344: 120–130.

PISEK A. & WINKLER E., 1959: Licht-und Temperaturabhängigkeit der CO_2–Assimilation von Fichte (*Picea excelsa* Link), Zirbe (*Pinus cembra* L.) und Sonnenblume (*Helianthus annuus* L.). *Planta*, 53(1): 532–550.

R CORE TEAM, 2018: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

RAFFA K.F., AUKEMA B.H., BENTZ B.J., CARROLL A.L., HICKE J.A., TURNER M.G. & ROMME W.H., 2008: Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience*, 58(6): 501–517.

RAMMIG A., FAHSE L., BUGMANN H. & BEBI P., 2006: Forest regeneration after disturbance: a modelling study for the Swiss Alps. *Forest Ecology and Management*, 222: 123–136.

SEIDL R., SCHELHAAS M.J., RAMMER W. & VERKERK P.J., 2014: Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, 4(9): 806–810.

SIPPOLA A.L. & RENVALL P., 1999: Wood-decomposing fungi and seed-tree cutting: a 40-year perspective. *Forest Ecology and Management*, 115: 183–201.

SPROULL G.J., ADAMUS M., BUKOWSKI M., KRZYŻANOWSKI T., SZEWCZYK J., STATWICK J. & SZWAGRZYK J., 2015: Tree and stand-level patterns and predictors of Norway spruce mortality caused by bark beetle infestation in the Tatra Mountains. *Forest Ecology and Management*, 354: 261–271.

STORAUNET K.O. & ROLSTAD J., 2004: How long do Norway spruce snags stand? Evaluating four estimation methods. *Canadian Journal of Forest Research*, 34(2): 376–383.

STREIT K., WUNDER J. & BRANG P., 2009: Slit-shaped gaps are a successful silvicultural technique to promote *Picea abies* regeneration in mountain forests of the Swiss Alps. *Forest Ecology and Management*, 257: 1902–1909.

SVOBODA M., 2005: Struktura horského smrkového lesa v oblasti Trojmezné ve vztahu k historickému vývoji a stanovištním podmínkám. *Silva Gabreta*, 11: 43–62.

SVOBODA M., FRAVER S., JANDA P., BAČE R. & ZENÁHLÍKOVÁ J., 2010: Natural development and regeneration of a Central European montane spruce forest. *Forest Ecology and Management*, 260: 707–714.

SVOBODA M., JANDA P., NAGEL T.A., FRAVER S., REJZEK J. & BAČE R., 2012: Disturbance history of an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. *Journal of Vegetation Science*, 23(1): 86–97.

VORČÁK J., MERGANIČ J. & SANIGA M., 2006: Structural diversity change and regeneration processes of the Norway spruce natural forest in Babia hora NNR in relation to altitude. *Journal of Forest Science*, 52(9): 399–409.

WILD J., KOPECKÝ M., SVOBODA M., ZENÁHLÍKOVÁ J., EDWARDS-JONÁŠOVÁ M. & HERBEN T., 2014: Spatial patterns with memory: Tree regeneration after stand-replacing disturbance in *Picea abies* mountain forests. *Journal of Vegetation Science*, 25(6): 1327–1340.

Zenáhlíková J., Svoboda M. & Wild J., 2011: Stav a vývoj přirozené obnovy před a jeden rok po odumření stromového patra v horském smrkovém lese na Trojmezné v Národním parku Šumava [The state and development of natural regeneration before and one year after a dieback in the tree layer of a mountain spruce forest in the Trojmezná area of the Šumava National Park.]. *Silva Gabreta*, 17: 37–54 (in Czech).
Zeppenfeld T., Svoboda M., DeRose R.J., Heurich M., Müller J., Čížková P., Starý M., Bače R. & Donato D.C., 2015: Response of mountain *Picea abies* forests to stand-replacing bark beetle outbreaks: neighbourhood effects lead to self-replacement. *Journal of Applied Ecology*, 52(5): 1402–1411.
Zielonka T., 2006: When does dead wood turn into a substrate for spruce replacement? *Journal of Vegetation Science*, 17: 739–746.

Received: 10 June 2020
Accepted: 11 August 2020