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Contrasting development of declining and living larch-spruce stands after a disturbance event: A case study from the High Tatra Mts.

Rôzny vývoj odumierania a prežívania smrekovcových smrečín po kalamite – prípadová štúdia z Vysokých Tatier

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Abstract
The decline of spruce stands caused by bark beetle outbreaks is a serious economic and ecological problem of forestry in Slovakia. In the preceding period, the decline affected mainly secondary spruce forests. Over the last decade, due to large bark-beetle outbreaks this problem has been observed also in natural spruce forests, even at high elevations. We dealt with this issue in a case study of short-term development of larch-spruce stands in the High Tatras (at a site called Štart). We compared the situation in the stand infested by bark beetles several years after the wind-throw in 2004 with the stand unaffected by bark beetles. We separately analysed the development of the mature (parent) stands and the regeneration. The results indicated that forest decline caused by bark beetles significantly depended on the stand structure (mainly tree species composition), which affected the period of stand disintegration. Mortality of spruce trees slowed down biomass accumulation (and thus carbon sequestration) in the forest ecosystem. In the new stand, pioneer tree species dominated (in the conditions of the High Tatras it is primarily rowan), although their share in the parent stand was negligible. The results showed different trends in the accumulation of below-ground and above-ground biomass in the declined and living stands. In the first years after the stand decline, rowan accumulated significantly more biomass than the main tree species, i.e. spruce. The reverse situation was under the surviving stand, where spruce trees accumulated more biomass than rowan. The different share of spruce and pioneer tree species, mainly rowan, affected the ratio between fixed (in woody parts of trees) and rotating (in foliage) carbon in the undergrowth. Forest die-back is a big source of carbon emissions from dead individuals, and the compensation of these losses in the form of carbon sequestration by future stands is a matter of several decades.

Key words: larch-spruce forests; mountain region; natural regeneration; declining stand; bark beetle outbreak

Abstrakt
Rozpad smrekových porastov spôsobený premnožením podkôrneho hmyzu predstavuje pre lesného hospodárstvo na Slovensku závažný ekonomický a ekologický problém. V predošlom období sa rozpad týkal hlavne nepôvodných smrečín. V ostatnom desaťročí sa vplyvom rozsiahleho premnoženia podkôrneho hmyzu takáto situácia zaznamenáva už aj v prirodzených smrekových porastoch, dokonca vo vysokých nadmorských výškach. Problematiku sme riešili formou prípadovej štúdie krátkodobého vývoja smrekovcovo-smrekového porastu vo Vysokých Tatrách (lokalita Štart). Porovnala sa situácia v lesnom poraste napadnutom podkôrnym hmyzom niekoľko rokov od vetrovej kalamity z roku 2004 s prežívajúcim (hmyzom neatakovaným) lesným porastom. Samostatne analyzujeme vývoj dospelého (materského) porastu a jeho obnovy. Výsledky naznačili, že na rozpad spôsobený podkôrnym hmyzom má podstatný účinok štruktúra porastu (hlavne drevinové zloženie), ktorá ovplyvňuje dobu rozpadu. Odumieranie smrekov spomalilo akumuláciu biomasy (teda aj viazaného uhlíka) v danom lesnom ekosystéme. V následnom poraste dominantne nastupovali prípravné dreviny (v podmienkach Vysokých Tatier je to hlavne jarabina), hoci ich zastúpenie v materskom poraste bolo zanedbateľné. Výsledky poukazujú na rozdielne tendencie vývoja akumulácie podzemnej a nadzemnej biomasy v rozpadnutom a prežívajúcom lesnom poraste. Jarabina v prvých rokoch po odumretí porastu akumulovala podstatne viac biomasy ako hlavná drevina, t. j. smrek. Opačná situácia bola pod prežívajúcim porastom, kde viac biomasy naakumulovali smreky než jarabiny. Rôzny podiel smreka a prípravných drevín, prevažne jarabiny, vplýva aj na pomer fixovaného (v drevných častiach stromov) a rotujúceho (v asimilačných orgánoch) uhlíka v podraste. Zánik lesného porastu znamená veľký zdroj emisie uhlíka z odumretých jedincov, pritom kompenzácia týchto strát v podobe absorpcie uhlíka prostredníctvom následného porastu je otázka niekoľkých desaťročí.

Kľúčové slová: smrekovcové smrečiny; horské oblasti; prirodzená obnova; odumieranie; napadnutie podkôrnym hmyzom

1. Introduction

Forest ecosystems continually change and evolve due to the establishment, growth and mortality of individual trees (or their groups). Biomass and hence carbon is accumulated in wooden tree components during growth. On the other hand, carbon stored in the foliage of deciduous tree species rotates on an annual basis, while in the case of "evergreen" tree species rotation occurs with a frequency of several years. After the death of trees, carbon is gradually released from all below-ground and above-ground components during

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the decomposition process. The most significant loss of carbon sequestration in forest stands occurs after their sudden destruction, most frequently caused by natural disturbances (e.g. Uriarte & Papaik 2007; Smithwick et al. 2009). Since forest ecosystems represent an important factor affecting carbon cycle, even at a global scale, their continuous existence is a condition for sustainable development of human civilisation (Bravo et al. 2008).

Nowadays, mountain forests in Slovakia with a high proportion of spruce are affected by an increased risk of disturbance by bark beetle outbreak. Although until recently large-scale decline occurred mainly in artificial spruce monocultures situated at lower elevations (e.g. in the Kysuce, and Spiš regions), extensive bark beetle outbreaks that occurred after the wind-throw in November 2004 have become dangerous also for semi-natural or natural spruce forests in the High Tatras (Fleischer et al. 2007; Nikolov et al. 2014). For example, Fleischer and Homolová (2011) reported higher biomass production in larch-spruce forests of the High Tatras (Fleischer 1999) in the late 20th century. High stand volume and its accumulation in the upper stand layer were one of the causes of the large-scale devastation of forests by the wind-throw in 2004. The destruction of larch-spruce stands by the wind-throw caused that the majority of these forests stopped being carbon "sink" and became carbon source.

The questions of active and passive management, naturalness or non-naturalness, functions and roles of bark beetles in the long-term development of these forests has been discussed for a long time (e.g. Strunz 1994; Koreň et al. 1997; Matějková & Jonášová 2004; Koreň 2005; Fleischer et al. 2007; Vakula et al. 2007; Jonášová et al. 2010). There are significant discrepancies between the proposals of solutions to this problem. The proposals vary from those suggesting no intervention in disturbed forest ecosystems up to those favouring complete processing of calamity wood followed by planting. For the proper management it is important to know the potential of natural regeneration. Kulla et al. (2009) presented the analysis of natural regeneration in declining spruce forests of the Kysuce region in Slovakia. The results from monitoring the state and the development of forest ecosystems after the wind-throw in the Tatras are presented by e.g. Šebeň (2010), Šmelková & Šmelko (2011), or Šebeň et al. (2011a, 2011b). In this region, not only the state of the wind-thrown parts was monitored, but also the state of the surrounding forest stands that had not been disturbed by wind, but were secondarily attacked and damaged by bark beetles, was assessed (Nikolov et al. 2014). Most of the authors presented promising findings about the sufficient amount of natural regeneration.

Similar results were presented also from the Šumava National Park, where an analogous situation to the one in the Tatras was observed a few years later. Although from the point of regeneration abundance, regeneration seems to be successful thanks to natural processes regardless of human intervention (e.g. Jonášová 2004; Ulbrichová 2004; Šebeň 2010; Štícha et al. 2013), the differences are mainly in the qualitative characteristics of regeneration, e.g. species diversity, height or age structure. The favourable state of natural regeneration confirmed by the abundant number of naturally regenerated individuals has also been reported from spruce forests under different management systems (e.g. Lin et al. 2012; Vencurik et al. 2013). Large variability in regeneration may be considered the greatest risk, as it complicates objective interpretation and generalisation of results. It is important to distinguish forests according to their current state and their future potential. At the same time, the state of endangered forests needs to be monitored in the long term, and the current and objective information on the state and the development of parent stands needs to be presented. Management interventions may mitigate the risk or consequences of bark beetle outbreak, before such a critical condition occurs. Apart from the need to monitor declining spruce forests, another reason for our case study was the lack of information about the current state of biomass stock (carbon) of tree species in both parent stands and the undergrowth.

The aim of the paper was to compare the development of a larch-spruce forest damaged by European spruce bark beetle with the state of a relatively undamaged stand. The paper compared not only the regeneration, but also the development of the parent stand mainly with regard to biomass stock and its inter-annual changes.

2. Material and methods

The research plots were established in the locality called "Start" situated about 2 km north-west of the village Tatranska Lomnica (High Tatras, Slovakia) in the year 2010. The forests at the site were not damaged by the wind-throw called "Elisabeth" in November 19, 2004, which destroyed a large area in the vicinity (Fig. 1). The site is located at elevations of 1,120 to 1,170 m, the aspect is south-east, and the slope is 10–20%. In this part of the High Tatras, climate is characterised by low mean annual temperatures (around 4.0 °C), high precipitation totals (almost 1,000 mm), and 140 days of snow cover (Vološčuk et al. 1994). The most common forest soils at the site are cambisols and podzols, and the bedrock is predominantly formed by granodiorite.

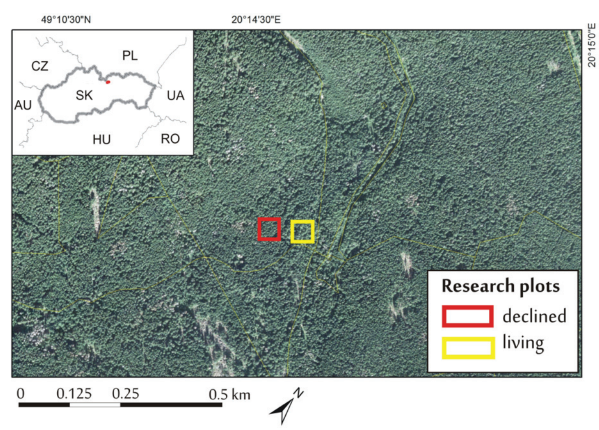

Fig. 1. Map of the site with the research plots.

Originally undisturbed alpine spruce stands were excessively damaged by bark beetles several years after the wind-throw causing their gradual die-back at large areas, which have significantly increased since 2008. Therefore, in 2010 two research plots of 50×50 m (0.25 ha) were established to compare forest development. One plot was established in a freshly attacked spruce stand with a high proportion of dead trees (declined forest, hereinafter as Plot D), and the second plot represented a stand, which has so far withstood the attack and the disintegration of the crown canopy (living forest, hereinafter as Plot L). Plot L is identical with the Level II intensive permanent monitoring plot (PMP), on which the health status has been monitored according to the methodology of ICP Forests (Pavlenda et al. 2014). The plot is one of the eight intensive monitoring plots in Slovakia. In this part of the High Tatras, dominant natural communities are of *Lariceto-Piceetum* forest type growing on acidic sites (according to EEA it is a Subalpine and mountainous spruce forest type). The oldest spruce and larch trees on the monitored plots were 140 years old. Since 2008, the increase of the number of dry dead trees and the occurrence bark beetles has been monitored at PMP (Pavlenda et al. 2014).

In 2010, the coordinates of all trees with a diameter at breast height (DBH) above 7 cm were measured at both plots D and L using Field-Map technology (IFER, Czech Republic). Tree state (living, or dead) was assessed, and its DBH and height was measured. Tree species was recorded (spruce, larch, and others with a small share were pine, fir and birch). Furthermore, the positions of crown projections of living trees were measured. Canopy cover was derived from the measured crown projections in the ArcView environment (Fig. 2). In 2010, the canopy cover derived from the measured projections was 61.8% and 8.0% at plots L and D, respectively.

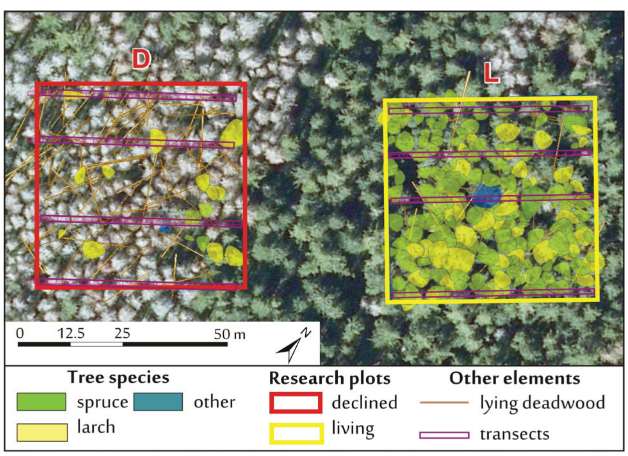

Fig. 2. Detailed situation at the research plots with measured trees, lying wood and regeneration transects (year 2010). Aerial photography is displayed in the background.

All pieces of lying coarse wood (dead lying trees with a top diameter above 7 cm) were measured – diameters at both ends and the length of log. All measured values were used for the accurate volume determination of living and dead trees (m^3), from which the biomass amount (kg) was derived.

Thin trees (regeneration) with a diameter below 7 cm were sampled on 4 transects, each 50 m long and 1 m wide (i.e. their total length at each plot was 200 m and their area was 200 m^2, which is 8% of the measured area of mature trees). The transects were located within the research plots at irregular spacing in such a way that they were in the direction of contour lines, and that they captured the regeneration variability in the parent stand. They were divided into 2 m sections, inside which the individuals of natural regeneration from seedlings up to those with the height of 2 m were thoroughly counted. The following tree species were identified: spruce, larch, fir, rowan, and birch. The following height categories were applied:

1. below 10 cm height, 2. from 10 to 20 cm, 3. 20–50 cm, 4. 50–100 cm, 5. 100–200 cm, 6. above 200 cm.

After the initial measurements in 2010, repeated measurements (diameters of mature trees, heights of individuals of natural regeneration) and assessments (status change of the mature trees) of living trees were performed in the following 2 years.

Apart from the empirically measured data the changes of the forest state was assessed using ortho-photos. We used the images of the Tatra region taken annually within the framework of the evaluation of post-disturbance development (NLC-ÚLZI), or other available ortho-photographs (Geodis-Eurosense) with acceptable resolution (from 0.5 to 1 m). We compared the images from the years 2005, 2007, 2009, 2012.

Data processing

The volume of standing (mature) trees was calculated using the national Slovak volume equations (Petráš & Pajtík 1991) for spruce, larch, pine, fir, and birch. From multiple possible volumes we used tree volume with bark representing the entire above-ground wood biomass (including stem and branches, and excluding stump, roots and foliage). The volume of lying dead wood was calculated using Smaljan formula. The biomass of thick trees was derived from their volume using the basic wood density of 0.45 for spruce and fir, and 0.50 for larch, pine, and birch (i.e. 1 m^{3} = 0.45 or 0.5 t of dry matter). The below-ground biomass was calculated using an allometric equation for spruce (Konôpka et al. 2011), derived from other datasets representing high elevation Norway spruce. The total biomass was obtained by summing the above-ground and below-ground biomass.

The biomass of thin trees (regeneration) was calculated using allometric equations for above-ground biomass, foliage, roots and total biomass (Pajtík et al. 2011; Konôpka et al. 2015). This was performed for individual height categories using the average height of a given category. The values calculated for individual transects were then summed up and converted to per hectare values. The final value representing a research plot was obtained as an arithmetic mean of 4 transects. Since the area of the research plots was known, all values were converted to per hectare values (m^3 ha^{-1}, or Mg ha^{-1}).

The data were processed and analysed in Microsoft Excel and ArcView.

3. Results and discussion

3.1 State and development of a parent stand

An intensive large-scale attack by bark beetles (with the dominance of *Ips typographus* L.) is obvious from the evaluation of the forest state based on the time sequence of aerial images. Figure 3 presents the development between 2005 and 2012 on the base of the four acquired images

(2005, 2007, 2009 and 2012). The first image shows the situation just after the wind-throw (2005), when the whole forest complex in the study area was healthy. The second image presents the situation one year before the massive outbreak (2007), when the monitored plot (plot D) was still in a relatively good condition, although some bark beetle focal points were already apparent in its western part and its surroundings. At Plot L, no signs of stand attack were visible. The rapid onset of bark beetle attack occurred during the years 2008 and 2009. In the last image from the year 2012, stand disintegration is already apparent, lying dead wood occurs at a greater part of the research plot attacked by bark beetles. Here we should note that the dead infested trees are best seen in the images, i.e. the actual infestation by bark beetles could occur a year earlier before it was visible in the image.

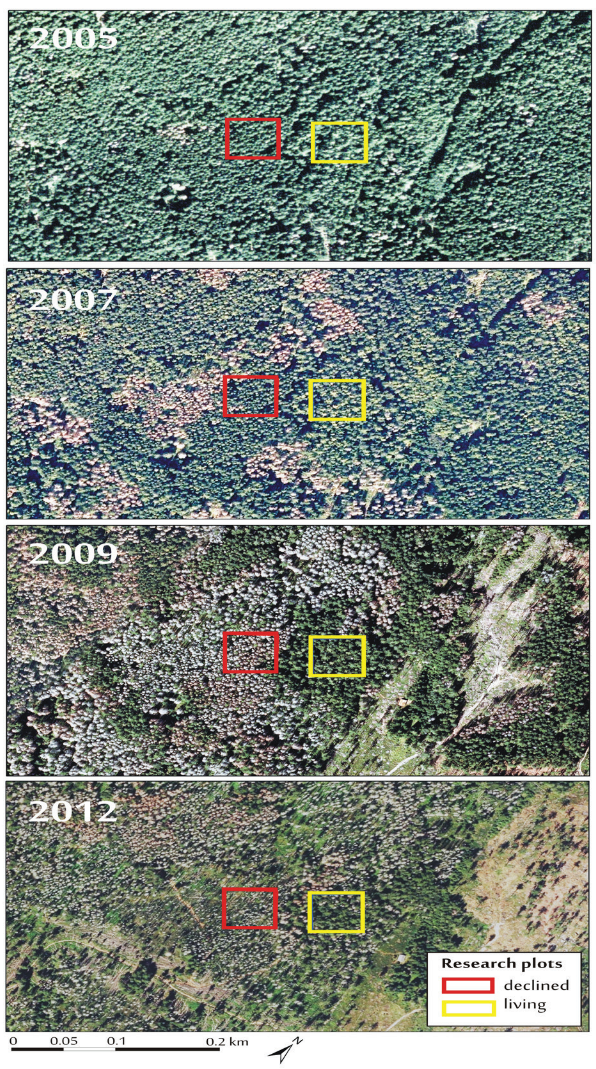

Fig. 3. Development of stand decline caused by bark beetles between 2005 and 2012.

The images present the rapid decline of the forest parts dominated by spruce. All trees at plot D practically died within two years after the occurrence of first infested trees in 2007. In the image from the year 2012 we can see bare areas with dead and uprooted trees. The development in the immediate vicinity (where Plot L is located) is different; this part of the forest has so far withstood the attack by bark beetles. Although we identified several trees infested by bark beetles, they were dispersed in the stand, and the area they covered in 2012 was negligible. A more detailed comparison of the infestation development at the plots from 2005 to 2012 (i.e. a time series of 8 years) is presented in Figure 4. The coverage data were derived from the visual interpretation of aerial images.

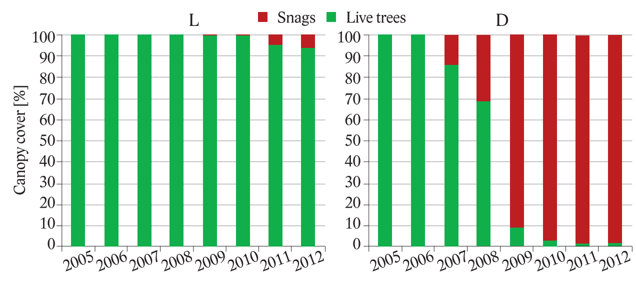

Fig. 4. Comparison of coverage of living and dead trees at the plots in the years 2005–2012 (visual evaluation of tree crowns in aerial images).

The graph (Fig. 4) documents the rapid progress of the infestation at plot D. While in 2007 the coverage of crown projections of dead trees was only 1/8 of the whole plot area, in 2009 (in two years) it was already 9/10. In the following few years, the decline has slowed down, most likely due to limited food sources of bark beetles, or as a result of weather conditions. Similar results were obtained by Nikolov et al. (2014) who recorded dramatic increase of forest area damaged by bark beetles in the High Tatra Mts. during the years 2007–2009. From the graph it is also obvious that spruce trees at plot L have withstood the attack of bark beetles. Until 2008, the stand remained undamaged (see also Fig. 3); the damaged parts first occurred in 2009, and in 2012 their share was around 6%.

The presented evaluation was based on the visual interpretation of aerial images referring to the aerial coverage. More precise and more detailed data were gathered by terrestrial measurements at both plots from 2010 to 2012. From these data it was possible to compare the changes in the number of living and dead trees, their basal area, wood volume and total biomass of the parent stand (Table 1). In comparison to the results presented above, some characteristics of stand structure could be determined more precisely, e.g. tree species composition (spruce, larch, other), and individual components of dead wood, i.e. lying and standing, which are difficult to detect in images. Table 1 presents several findings:

– At the beginning of the measurements, the total number of trees including dead standing and lying trees was similar at both plots. Over the time, the proportion of the number of living trees decreased from around 60% to 50% at plot L, while at plot D it remained at a level of only 6%. At plot D, approximately 2/3 of all trees were dead standing trees, and around 1/4 were dead lying trees. At the beginning of the measurements, spruce proportion at plots L and D was 82 and 94% from total trees, respectively.
– From the point of the initial basal area, both plots were comparable. Over the time, basal area at the undisturbed

plot L slightly increased, whereas at plot D it remained almost constant. In contrast to the proportion calculated from the number of trees, spruce share in basal area changed; at plot L it was only 60%, whereas at plot D it remained at 95%.

– The contrasting state of the two plots is even better reflected by the above-ground volume. This parameter is by about 1/3 smaller at plot D than at plot L. This can mean either lower production or loss of wood biomass caused by mortality, and dead wood decomposition. The proportion of spruce at plot L calculated from volume was reduced to 52%, while at plot D it decreased only to 92%. However, if the share was expressed from the living trees, the results varied considerably from those presented. At plot L, more volume of living trees belonged to larch than to spruce. At plot D, larch share was 87% of volume of living trees. The total above-ground biomass increased at plot L by about 1% (from 505 to 514 Mg ha^{-1}) in 2 years, while at plot D it remained unchanged due to a small number of living and still growing trees.
– From the point of carbon fixation in tree species, we can obtain the most pertinent information by comparing the total biomass amount (above-ground and below-ground) between the plots. Biomass amount is significantly affected by tree species composition and the developmental changes (increment versus mortality). At the disturbed plot D, no changes in biomass amount occurred during the assessed period, while at the surviving plot L we recorded a small increment (+2%). The proportion of larch increased to 45% at plot L due to its greater timber density, while spruce share was about 50% of the total biomass. The share of larch increased also at plot D from the initial 4 and 6% calculated from the number of trees or basal area, respectively, to 8%. When the share was calculated from the biomass of living trees, larch proportion was 51% and 84% at plots L and D, respectively.

It is obvious that while the biomass amount of spruce was similar at both plots L and D, plot L, which has been resistant to bark beetles, had a greater proportion of larch. Larch is known as a stabilising component in homogeneous spruce stands, not only against abiotic harmful factors (wind, snow), but also against biotic factors, particularly bark beetles. After spruce dies out in larch-spruce stands due to bark beetle attack, the share of larch increases. The analysis of tree species composition at both plots clearly showed that the higher proportion of larch significantly hindered the risk of decline of natural larch-spruce forests. At plot D, where larch share was less than 10%, a complete destruction of the parent stand was observed within a couple of years. In general, European larch is considered as a stand stabilising species with very high resistance to abiotic harmful agents as well as pests (Vakula et al. 2015).

Development of stands over the years 2010–2012

The comparison of the changes in the total biomass of both stands is illustrated in figure 5. Apart from the lower value of biomass at plot D, we can also see that during the 3 monitored years no changes in biomass amount occurred at this plot. At plot L very small changes were observed, where the total

Table 1. Development of basic characteristics of monitored stands in the categories of living trees, snags and lying dead wood over the years 2010–2012.

Research plots	Species	Year	Number of trees n ha^{-1}				Basal area m^2 ha^{-1}				Aboveground volume m^3 ha^{-1}				Total biomass* Mg ha^{-1}			
			Living	Snag	Lying	Total	Living	Snag	Lying	Total	Living	Snag	Lying	Total	Living	Snag	Lying	Total
Living forest (Plot L)	Spruce	2010	632	332	196	1,160	31.3	10.1	11.0	52.4	340	95	28	462	185	53	16	253
	Larch		168	48	4	220	29.1	2.1	0.5	31.8	365	16	3	384	218	10	2	230
	Others		24	0	4	28	3.0	0.0	0.3	3.3	36	0	1	37	22	0	1	22
	Total		824	380	204	1,408	63.5	12.2	11.8	87.5	741	110	33	884	424	63	19	505
	Spruce	2011	532	432	196	1,160	25.0	16.9	11.0	52.8	263	175	28	466	144	96	16	255
	Larch		164	52	4	220	28.5	3.0	0.5	32.0	357	27	3	387	213	17	2	232
	Others		24	0	4	28	3.1	0.0	0.3	3.4	37	0	1	38	22	0	1	23
	Total		720	484	204	1,408	56.5	19.9	11.8	88.2	657	202	33	891	379	113	19	510
	Spruce	2012	532	432	196	1,160	25.3	16.9	11.0	53.2	266	175	28	470	145	96	16	257
	Larch		164	52	4	220	28.8	3.0	0.5	32.3	360	27	3	390	215	17	2	234
	Others		24	0	4	28	3.1	0.0	0.3	3.4	37	0	1	38	22	0	1	23
	Total		720	484	204	1,408	57.3	19.9	11.8	88.9	664	202	33	899	383	113	19	514
Declined forest (Plot D)	Spruce	2010	20	976	388	1,384	0.9	59.8	32.8	93.5	4	526	96	625	3	299	54	355
	Larch		52	32	4	88	3.6	0.7	0.1	4.4	45	7	0	53	26	4	0	31
	Others		4	0	0	4	0.3	0.0	0.0	0.3	3	0	0	3	2	0	0	2
	Total		76	1,008	392	1,476	4.8	60.5	32.9	98.2	52	533	96	681	31	303	54	387
	Spruce	2011	20	976	388	1,384	0.9	59.8	32.8	93.5	4	526	96	625	3	299	54	355
	Larch		52	32	4	88	3.6	0.7	0.1	4.4	45	7	0	53	26	4	0	31
	Others		4	0	0	4	0.3	0.0	0.0	0.3	3	0	0	3	2	0	0	2
	Total		76	1,008	392	1,476	4.8	60.5	32.9	98.2	52	533	96	681	31	303	54	387
	Spruce	2012	20	976	388	1,384	0.9	59.8	32.8	93.5	4	526	96	625	3	299	54	355
	Larch		52	32	4	88	3.6	0.7	0.1	4.4	45	7	0	53	26	4	0	31
	Others		4	0	0	4	0.3	0.0	0.0	0.3	3	0	0	3	2	0	0	2
	Total		76	1,008	392	1,476	4.8	60.5	32.9	98.2	52	533	96	681	31	303	54	387

* Note: Total biomass represents all tree above- and below-ground components except for the above-ground part of stump, secondary branches and foliage.

biomass increased from 505 to 514 Mg ha^{-1} over 2 years. Over the same time, about one-tenth of the total number of trees in the stand died (transition of living biomass to standing snags).

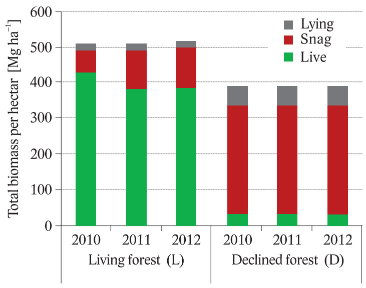

Fig. 5. Total tree biomass in the period 2010–2012.

If we looked at the changes in the biomass of individual tree species (Fig. 6), we found inter-annual changes at plot L. In the case of spruce, we recorded a significant decrease in the living biomass by 41 Mg ha^{-1} between the years 2010 and 2011, while the increase in the biomass of dead trees was 43 Mg ha^{-1}, i.e. the increment was 2 Mg ha^{-1}. Between the years 2011 and 2012 we observed an increase in spruce biomass by 4 Mg ha^{-1}; no new dead trees were observed at the plot. Between 2010 and 2012 we observed the decrease in the biomass of larch by 5 Mg ha^{-1}, and mortality of spruce trees with the biomass of 7 Mg.ha^{-1} (i.e. total increment in biomass was 2 Mg ha^{-1}). In the following year, we observed a total increase in biomass by 2 Mg ha^{-1}, while no biomass transition from living to dead trees was detected.

3.2. State and development of regeneration

Number of regenerated individuals

At either of the plots, tree species composition of a future stand did not correspond with the tree species composition

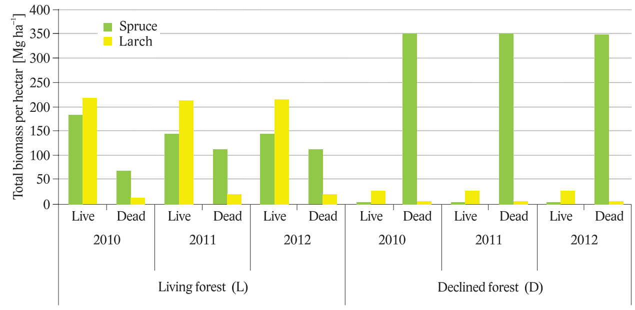

Fig. 6. Changes in total biomass of spruce and larch at plots L and D in the period 2010–2012.

of the parent stand. Although spruce was a substantial component of the parent stand and regeneration, larch as the second main tree species was absent in regeneration. From more than 800 regenerated individuals recorded in 2010, only one was larch with a height below 10 cm, which did not occur in the following years. Rowan, a pioneer tree species, had a high proportion in regeneration, although it did not occur in the parent stand. Apart from spruce and rowan, which were most common tree species in regeneration, several individuals of fir and birch were also recorded. Here we analysed only the most represented tree species – spruce and rowan, which together constituted 99.5% of the number of recorded individuals in 2010 and 2012 (Table 2).

Overall, we identified a relatively large number (density) of regenerated individuals at both plots. The largest part of regeneration were the individuals in the smallest category, i.e. individuals with a height below 10 cm. They do not represent secured regeneration, and this fact was also reflected in the inter-annual fluctuations of the numbers. Furthermore, great spatial variability (between the individual sub-plots with an area of 4×2 m, as well as between the four transects) was typical for the regeneration. The variability is in the table represented by the standard deviation. The standard devia-

Table 2. Average numbers of regenerated individuals (thousand pcs ha^{-1}; average ± standard deviation) at research plots L and D in the years 2010–2012.

Plots	Year	Species	Height category < 10 cm	10–20	20–50	50–100	100–200	>200 cm	Total
Living forest	2010	Spruce	18.5 ±21.7	2.6 ±5.1	0.4 ±2	0.3 ±1.6	0.2 ±0.9	0 ±0	21.9 ±24.9
		Rowan	0.1 ±0.5	0.1 ±1	0.4 ±1.9	0.3 ±1.3	0.1 ±0.5	0 ±0	0.8 ±3.8
		Total	18.6 ±21.2	2.7 ±5.1	0.8 ±2	0.6 ±1.3	0.2 ±0.4	0 ±0	22.7 ±21.1
	2011	Spruce	15.2 ±21.4	1 ±3.2	0.4 ±2.2	0.2 ±1.2	0.2 ±0.9	0 ±0	16.9 ±22.6
		Rowan	0.4 ±4	0.2 ±1.1	0.4 ±1.8	0.6 ±3	0.5 ±4.1	0.1 ±0.5	2.1 ±8.5
		Total	15.6 ±17.4	1.1 ±2.1	0.8 ±0.4	0.8 ±1.8	0.7 ±3.3	0.1 ±0.5	18.9 ±14.1
	2012	Spruce	8.2 ±12.6	2.2 ±5.1	0.6 ±2.3	0.3 ±1.1	0.2 ±0.9	0.1 ±0.5	11.4 ±15.8
		Rowan	0.6 ±3.3	0.1 ±0.5	0.3 ±1.8	0.3 ±1.9	0.5 ±4	0.1 ±0.5	1.7 ±6.5
		Total	8.8 ±9.2	2.2 ±4.6	0.8 ±0.6	0.6 ±0.8	0.6 ±3.2	0.1 ±0	13 ±9.3
Declining forest	2010	Spruce	13.1 ±21	3.2 ±8	0.3 ±1.1	0.2 ±0.9	0.1 ±0.5	0 ±0	16.7 ±25
		Rowan	0 ±0	0.2 ±0.9	0.7 ±3.2	0.4 ±2.2	0.3 ±1.4	0 ±0	1.6 ±5.4
		Total	13.1 ±21	3.3 ±7.1	1 ±2.1	0.6 ±1.4	0.4 ±0.9	0 ±0	18.2 ±19.6
	2011	Spruce	8 ±15.9	0.3 ±1.7	0 ±0	0.4 ±2.8	0.1 ±0.5	0 ±0	8.7 ±16.8
		Rowan	0 ±0	0 ±0	0.4 ±1.8	1.1 ±3.5	1.7 ±6.2	0.1 ±0.5	3.2 ±7.9
		Total	8 ±15.9	0.3 ±1.7	0.4 ±1.8	1.5 ±0.6	1.7 ±5.7	0.1 ±0.5	11.9 ±8.8
	2012	Spruce	4.8 ±11.4	2.8 ±12.7	0.8 ±5.3	0.6 ±4.1	0.1 ±1	0.1 ±0.5	9.1 ±23.3
		Rowan	0.1 ±0.5	0.1 ±0.7	0.1 ±0.5	0.4 ±1.5	0.9 ±3.5	0.3 ±2.1	1.8 ±4.6
		Total	4.8 ±10.9	2.9 ±12	0.9 ±4.8	1 ±2.6	1 ±2.5	0.4 ±1.6	10.9 ±18.7

tion of most categories more or less equals their average values. This fact must be taken into account, which reduces the possibility of generalising the results measured at the site.

Inter-annually, we observed a decrease of the average number of regenerated individuals at both plots, which was mainly caused by spruce trees with a height below 10 cm. At the beginning of the monitoring, their share in the total number of regenerated individuals was 70–80% at both plots. Gradually, their proportion was reduced due to their natural (competition-induced) mortality. After two years, only about a half of the initial number was observed. The development in the higher height categories is more important. No significant trends were revealed at plot L, although some non-significant inter-annual fluctuations (the increase of the number of rowan individuals) were observed. At plot D, we observed a slight shift of spruce and rowan individuals into higher height categories, but due to the great variability in the numbers, the changes cannot be generalised.

Even in the relatively short period, i.e. during the three years, we observed some differences between the tree species in higher categories. While in the category with a height below 10 cm (seedlings) spruce dominated with a share of 86–98% every year, in the category with a height above 50 cm the ratio between the number of spruce and rowan individuals was balanced. In 2011, rowan prevailed at both plots, but much more at plot D. In 2012, this trend became even more pronounced. This finding is in accordance with the results by Myking et al. (2013) who showed that rowan competed over other species especially in open areas and gaps of forest stands.

Biomass of regenerated individuals

Different trends in the development of above-ground biomass of regenerated individuals between the research plots are relatively clear (Fig. 7). In contrast to the presented decreasing trends in the number of individuals (due to mortality of less competitive individuals), the above-ground biomass was increasing (increment of more competitive individuals). While in the living stand at plot L, where the canopy coverage of the parent stand shaded the regenerated individuals (60–70%), spruce dominated during the whole monitored period, in the declining stand at plot D spruce was dominant only in 1st monitoring year, i.e. 1–2 years after decline. In the following year, the value of the above-ground biomass of rowan was three times higher than of spruce. In the third monitoring year, biomass of spruce at plot D increased by threefold compared to the year 2011, but rowan continued to lead over spruce.

The total amount of above-ground biomass in spruce regeneration was about 100 kg ha^{-1} at plot L in the first year, while at plot D it was less than 50 kg ha^{-1}. Over 2 years, it increased to 220 kg ha^{-1} at both plots. Greater increments were observed for rowan; in 2010 its biomass amount in regeneration was less than 50 kg ha^{-1} at either of the plots, and increased to approximately 100 kg ha^{-1} at plot L. At the declining plot D, the biomass amount of rowan increased to 220, and in the following year to almost 350 kg ha^{-1}. For instance, Konôpka et al. (2015) estimated the aboveground biomass of a young stand after the wind-throw in the High Tatras. The biomass was around 700 kg ha^{-1} and 1000 kg ha^{-1} in the years 2013 and 2014, respectively. These numbers are higher than those from plots L and D, because Konôpka et al. (2015) focused on the stands growing under fully open area conditions nine and ten years after the wind-throw.

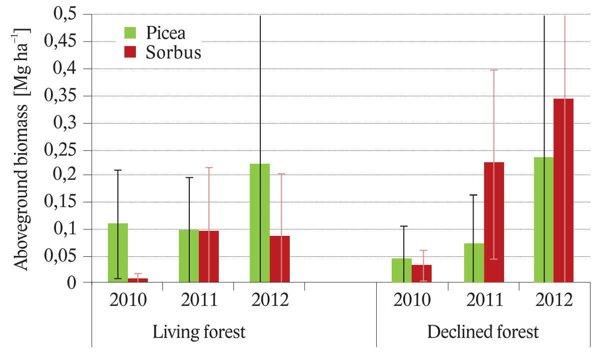

Fig. 7. Average per hectare above-ground biomass of regeneration (bars represent standard deviation) at plots L and D in the period 2010–2012.

Figures 8, 9, and 10 present the changes in the biomass amount of foliage, below-ground biomass and total biomass of regenerated individuals. Spruce accounted for more biomass of foliage (needles/leaves) at both plots, while rowan had greater amount of below-ground biomass. The total biomass corresponded with the above-ground biomass, while the total biomass of spruce and rowan was by about 20–30% and 40–50% higher than the above-ground biomass, respectively.

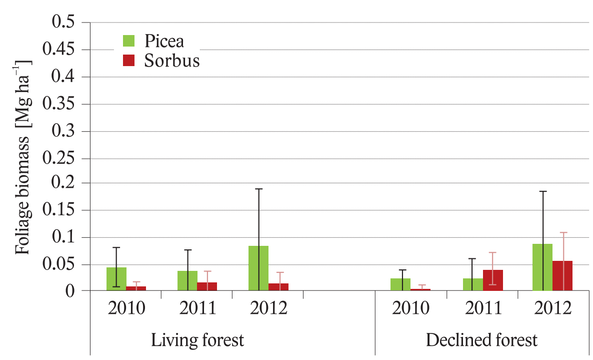

Fig. 8. Average per hectare biomass of foliage of regenerated spruce and rowan at plots L and D in the years 2010–2012.

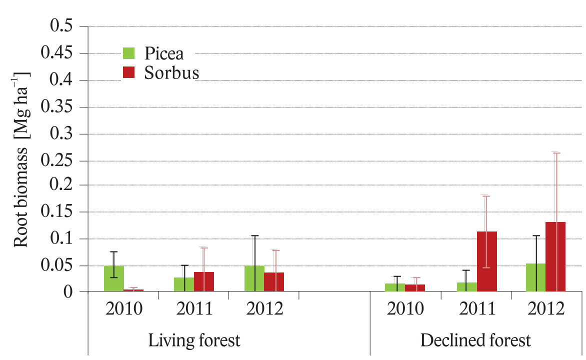

Fig. 9. Average per hectare below-ground biomass of regenerated spruce and rowan at plots L and D in the years 2010–2012.

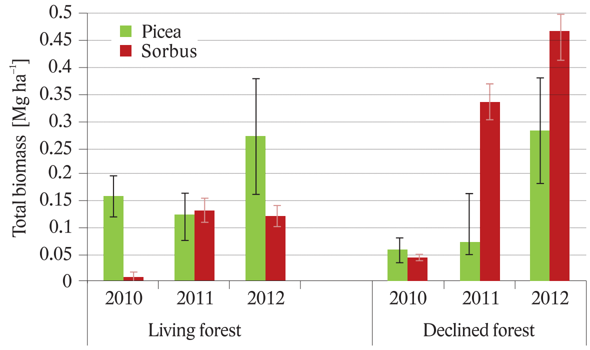

Fig. 10. Total biomass of regenerated spruce and rowan at plots L and D in the years 2010–2012.

The results indicate that shortly (i.e. after a few years) after the forest decline, dead trees (snags, and lying dead wood) were the most important elements of temporary carbon sequestration. This refers to both their above-ground and below-ground parts. During the first years after the forest decline, regeneration participates in carbon fixation only at a small rate (in our case, i.e. at plot D by only 1–2 per mille). Nevertheless, the inter-annual increase in regenerated biomass of both spruce and rowan was very dynamic. In the case of young trees, significant differences in biomass allocation were revealed between spruce and rowan. While spruce allocated more biomass in needles, rowan rotated more carbon through this component due to its annual leaf turnover. This inter-species difference indicates different growth strategies of monitored tree species, and also some differences in the ratio between the long-term sequestered and rotated carbon. Similar differences between spruce and broadleaved species (beech) in the stage of advanced regeneration and thicket were presented by e.g. Konôpka et al. (2013).

The results also indicate that forest decline is a big source of carbon emissions from dead individuals, and the compensation for these losses in the form of carbon sequestration by future generations is a matter of several decades. However, at the same time we must not forget the changes in the "behaviour" of carbon stored in the soil, since disturbances usually stimulate its emissions to the air (e.g. Kramer et al. 2004). A complex solution requires long-term research aimed at examining the development of carbon stocks in vegetation (not only in trees, but also in other plants) and in soil (see e.g. Liu et al. 2011).

4. Conclusions

Larch-spruce forests growing in the High Tatras represent specific communities. Forests situated at lower elevations of 900–1,200 m a.s.l. are most frequently affected by repeated large-scale wind-throws. Under certain conditions, the wind-throws are followed by bark-beetle outbreaks on unprocessed wood mass and the die-back of the surrounding forests. Susceptibility and resistance, extent of damage as well as the time of forest decline of the stands damaged by bark beetles depends on the stand structure. Apart from the age (older spruce stands are more susceptible), species composition is also important, namely the ratio of spruce to other tree species. From other species, larch is most frequent in the studied communities of the High Tatras.

The case study analysed multi-annual development of larch-spruce forests on the base of the two research plots (living-L and declined – D). Although the site was not directly affected by the wind-throw in November 2004, bark beetle outbreak occurred here as a secondary process causing the destruction of the surrounding stands. The massive onset took place between 4th and 5th year after the wind-throw. While plot L with the high proportion of larch (15% of the number of trees, 36% of basal area, 43% of aboveground volume, and up to 45% of the total biomass) withstood the attack for several years (8 years after the wind-throw the proportion of infested trees did not exceed 10% of the plot area), plot D was practically dead already five years after the wind-throw (the proportion of the infested trees exceeded 90%). In spite of the fact that the number of trees and basal area of both plots were comparable, larch proportion at plot D was only 5–8% (the smallest value was calculated from the basal area, and the highest from the biomass). Due to spruce decline at the plot, the proportion of larch in the living biomass increased over the last few years to more than 80%. Although during the three years of measurements of individual components (living trees, standing snags, lying coarse woody debris) the recorded changes primarily accounted for the shift from the living trees to snags, and for the increment of living trees, the total biomass amount was permanently balanced at both plots, and mainly comprised the biomass of the parent stand. The biomass in the living forest reached almost 900 Mg ha^{-1} (biomass proportion of living trees decreased from 80 to 70%), while in the declined forest it was below 700 Mg ha^{-1} (and the proportion of living trees was permanently less than 10%). The proportion of living below-ground biomass of mature trees was approximately 20–26% of the above-ground biomass, while in the living forest it was around 20%, and in the declined one it was about 25%. Higher proportion of the living below-ground biomass was caused by the dominance of larch characterised by denser wood.

Monitoring of regenerated individuals revealed their high average number of 10–20 thousand pieces per hectare, of which the unsecured spruce seedlings with a height below 10 cm had a dominant share. Due to their gradual mortality caused by natural competition or shading, a significant decrease from 20 to 13 thousand per ha, or from 13 to 8 thousand was recorded after 2 years. Nevertheless, this amount of regeneration is still sufficient. Spruce as the main tree species was very abundant in regeneration, but other main tree species (larch, fir) occurred only rarely; this is contrary to the tree species composition of the parent stand. On the other side, rapid development of pioneer tree species – predominantly rowan, and individually also birch, and aspen, was observed.

The development of regeneration biomass indicates its increase. This is more reflected in the favour of pioneer tree species (rowan), which had a similar number of trees as spruce at higher height categories, but accumulated significantly more biomass. Over 3 years, the above-ground biomass of regeneration increased from 0.1 to 0.3 Mg ha^{-1} at plot L (living forest), while in the declined forest (plot D) the accumulation was far more pronounced from 0.1 to 0.6 Mg ha^{-1}.

When we compared foliage biomass, spruce outweighed rowan, while in the case of below-ground biomass, rowan outweighed spruce.

The revealed facts are important not only for the selection of optimal management after disturbance, but also for the decision making in the cases where it is still possible to prevent bark beetle outbreak (active forest protection). Although in the new stand the biomass increment of the dead forest was twofold greater than the one of the living forest (formed mainly by the expansion of rowan as a pioneer tree species), the comparison of absolute values of biomass showed that the biomass of the regeneration was still several hundred times (!) lower than the biomass of the mature standing forest (0.1–0.6 Mg ha^{-1} compared to 300–350 Mg ha^{-1} or 26 Mg ha^{-1} in the declined forest). The prevention of forest decline may stabilise a huge quantity of living biomass (in our case around 350 t of dry matter per ha, which is almost 180 t carbon per ha). Moreover, the prevention of forest die-back also eliminates the potential increase in carbon emissions from soil.

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