Article

Forest Regeneration Patterns Differ Considerably between Sites with and without Windthrow Wood Logging in the High Tatra Mountains

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Abstract: Our research focused on the impact of post-disturbance management on the subsequent forest stands in the territory of the High Tatra Mts. situated in the northern part of Slovakia. The field work was carried out within the post-disturbance area in 2019, i.e., 15 years after the windstorm. In total, we used data from 80 monitoring plots (MP): 40 plots situated inside the managed part and 40 in the unmanaged areas. Post-disturbance management specifically consisted of logging of wind-thrown wood; therefore, the main difference between the two areas (salvaged versus unsalvaged) was the amount of coarse woody debris (CWD) left on site. We focused on the characteristics of newly regenerated forest stands: the number of trees and tree species per MP, tree height and browsing (mostly by red deer, *Cervus elaphus*) were recorded as was their growth substrate, i.e., soil or CWD. Higher tree densities, larger trees as well as higher tree species richness were found at salvaged plots. In addition, more evident dominance of Norway spruce (*Picea abies* (L.) Karst.) was recorded at unsalvaged plots. Common rowans (*Sorbus aucuparia* L.) were frequent at both plot types. Birch trees (*Betula* sp.) were very frequent at salvaged plots, while only a few birch individuals were recorded at unsalvaged ones. The proportion of trees growing on CWD was 15% at unsalvaged and 3% at salvaged plots. Trees growing on the soil contained nearly double the aboveground biomass than those on CWD. Red deer browsing was approximately two times more frequent at salvaged than unsalvaged plots. While rowan was extremely prone to browsing, spruce was damaged negligibly. These main findings could have two contradictory conclusions, the positive one being that differentiated post-disturbance management within a certain area can combine both forestry and nature conservation interests. Moreover, it can generate parallel forests with different properties that might positively influence the future stability of forest ecosystems as a whole. The negative side might be that contrasting post-disturbance management can cause an uneven distribution of red deer population and intensive browsing in areas favourable for game.

Keywords: post-disturbance forest regeneration; sustainable forest management; tree species composition; tree height; tree biomass; coarse woody debris; game browsing

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1. Introduction

In the prevailing part of boreal and temperate forests in Europe, large-scale disturbances have been occurring with an increasing tendency over the last two to three decades [1]. At the same time, the increasing contribution of wind to the total volume of disturbed wood has been observed, especially in Central, Northern and Western Europe [2]. In the present millennium, the largest and most destructive storms in Central Europe were “Kyril” (17–19 January 2007) and “Emma” (28 February–2 March 2008), which damaged

large areas of forests, especially in Germany and Czechia [3]. The storms destroyed several tens of millions m³ of forest in those countries. However, the worst European windstorm within the available historical records was cyclone “Lothar” (on 26 December 1999), which crossed France, Belgium, Luxemburg and Germany. The storm caused forest destruction equalling nearly 200 million m³ of wood [4]. Later, a study on post-disturbance forest development after these windstorm episodes proved a close interaction between wind and bark beetle damage in forests, which is amplified by ongoing climate change [5].

The risk of wind disturbance in forests increases not only with the increasing severity of the harmful agent (a consequence of climate change [6]), but also with decreasing forest stability, i.e., resistance to wind destruction [7–9]. The risk of disturbance is increased with accumulating aboveground biomass stock in forest stands, and at the same time, more wood volume per hectare is obviously damaged in a single disturbance episode [10].

Long-term records from Slovakia demonstrated that large-scale disturbances of forests have been increasing especially since the beginning of the third millennium [11]. Moreover, the evidence shows that a windstorm has been the most destructive agent in most observation years. In the present millennium, the largest windthrow in Slovak forests occurred in November 2004 (windstorm “Elisabeth”, see [12]). The wind hit northern and central regions of the country in particular, with the epicentre of forest destruction in the High Tatra Mts. and the Podtatranska Basin (most of the disturbed area belonged to the Tatra National Park, TANAP hereinafter). Before the disturbance, these regions had prevalingly been covered with forests for 60 years [13]. Those forests were dominated by Norway spruce (*Picea abies* L. Karst), which represented over $\frac{3}{4}$ of the wood stock there at the end of the last century [14]. However, under the conditions of Central Europe, mature spruce stands are the most prone to wind damage of all forest types (e.g., [8]).

Wind destruction of forests brings a variety of negative consequences to forest ecosystem services [15] and disrupt sustainable forest management (often associated with the term “continuous cover forestry”, i.e., [16]). At the same time, large-scale disturbances can cause difficulties in forest restoration, which is always an urgent task in terms of providing sustainable forest cover. Obviously, once a forest is destroyed, treeless areas would be reforested either by natural regeneration from local seed dispersal and/or by human intervention in the form of tree planting. Even though post-disturbance development of vegetation is important for the future of forest stands, our knowledge about this growth phase of forests is still rather scarce (e.g., [17]). Researchers should intensify studies in this field and enhance their understanding concerning the drivers of these processes in post-disturbance forest stands, especially with regard to the recently increasing frequency and severity of forest destructions (i.e., increasing extent of recent large-scale post-disturbance areas). Thus, regularities of natural disturbances would be understood and some of their principles adapted as a part of sustainable forest management [18].

Usually, the first step of post-disturbance management is the logging of calamity wood, especially of merchantable stem wood [19]. However, this kind of operation is not possible in hardly accessible terrain or in areas with high levels of nature conservation, mainly in national parks. Thus, in such conditions calamity wood remains on site and forms coarse woody debris (CWD), which creates habitats for a variety of plant and animal species [20]. Many authors indicated a positive role of CWD for tree regeneration (e.g., [21–26]) and noted that growth conditions for seedlings improve with its decay. Unfortunately, works focusing on relatively fresh CWD (in a very early stage of decomposition) as the environment for forest regeneration are scarce. In some cases, negative effects of CWD on natural regeneration might be expected due to, e.g., space limitation, decrease in light available under CWD, etc. Papers focusing on the role of CWD in a certain degree of decay prevalingly supported positive ecological, especially climatic, and nutritional conditions for seedling growth [22–27]. Moreover, lying logs can protect seedlings from competitive herbs [28] and even to game browsing, to some extent [29]. Most authors [19,30,31] commented that salvage logging reduces plant diversity and leads to their structural and functional homogenisation. However, a large-scale satellite study from Central Europe

demonstrated a lower recovery rate in unsalvaged than in salvaged forest areas [32]. So far, there is no definitive knowledge concerning the effects of post-disturbance management, including both wood logging and tree planting on development as well as on the properties of the consecutive forests, especially from a long-term perspective. We believe that post-disturbance management should be related not only to natural conditions (e.g., forest regeneration potential [33,34]), but mainly to specific demands of local people for forest roles—especially if considering protected versus commercial forests [35].

The main aim of this paper was to compare forest regeneration patterns between sites with and without logging of wind-thrown wood in the TANAP. Furthermore, we wanted to quantify the importance of wind-thrown wood that remained on site (lying stems, stumps and root plates) for the existence and development of young trees as well as the frequency of game browsing at both sites (with and without logging wind-thrown wood, i.e., salvaged and unsalvaged).

2. Materials and Methods

2.1. Study Area

The fieldwork was carried out in the territory of the TANAP, which is situated in northern Slovakia. The bedrock is predominantly formed by sediments of granodiorites. Forest soils are prevailingly lithic leptosols and podzols. Because of relatively high altitudes, the climate is typically cold (the annual mean temperature is about 5.0 °C) and moist (annual precipitation total is over 1000 mm), and snow cover lasts around 120 days [14]. The area is mostly covered by fully stocked forests up to approximately 1600 m a.s.l., followed by stands composed mostly of mountain pine (*Pinus mugo* Turra) and scattered rowans (*Sorbus aucuparia* L.), growing up to approximately 2000 m a.s.l. [14].

Our research focused on the post-disturbance area after the destruction caused by a windstorm. Before the disturbance, these regions were prevailingly covered with spruce-dominant forests aged between 61 and 120 years [36]. A substantial part of the spruce-dominated forests in this area was destroyed by a devastating windstorm, “Alžbeta”, on November 19th, 2004 (see [12]). The main portion of damaged forests occurred between 700 and 1200 m a.s.l, while most trees were uprooted, and stem breakage occurred only occasionally. Undamaged stands remained in the epicentre of wind disaster only sporadically, and usually comprised individuals of European larch (*Larix decidua* Mill.) and Scots pine (*Pinus sylvestris* L.), a greater portion of which survived than Norway spruce.

To monitor the post-disturbance development of forest stands in the area, specialists of the National Forest Centre (NLC) established a network of 90 monitoring spots (MSs) in a regular grid of 1.0 × 1.0 km in 2007. A tree inventory was repeatedly performed in 2010, 2016 and 2019 (see [13,37]). This paper presents results originating exclusively from field measurements performed in 2019.

Here, we briefly explain post-disturbance forest management in the area. The post-disturbance area was managed in contrasting ways regarding the degree of nature protection, specifically: (a) partly logged (approx. 1/3–2/3 of merchantable wood) or wholly processed merchantable wood; referred to as a salvaged area hereinafter, or (b) fully excluding wood logging; referred to as an unsalvaged area hereinafter. The majority of the wood was processed within two years after the disturbance (2005–2006). Similarly, different approaches with respect to the level of nature protection were implemented for forest regeneration. For 2–6 years after the wind destruction, nearly a half of the recovered area was secured by planting, in particular, European larch, Norway spruce, Scots pine, sycamore (*Acer pseudoplatanus* L.) and silver fir (*Abies alba* L., see [38]). This was performed within salvaged areas, but only at lower altitudes. At higher altitudes artificial reforestation was very scarce, even in the areas where calamity wood was processed. On the other hand, unsalvaged areas were left to natural succession, regardless of altitude.

Our analyses of the data collected in 2016 showed that the number of MSs located in the unsalvaged areas was very low (only 8 out of a total of 90). Therefore, in 2019, we decided to intensify the inventory with a denser grid of MSs, specifically 0.25 × 0.25 km.

This resulted in 20 MSs (6 former and 14 new) in the unsalvaged areas and a further 20 MSs were established within the salvaged areas (Figure 1). All MSs situated inside the unsalvaged areas were selected close to the MSs located in the salvaged areas, to ensure spatially comparable sets. The MSs with post-windthrow logging were situated at very similar altitudinal conditions as those without logging (Table 1). Previous studies [36] showed that the amount of coarse woody debris (data covered only standing and lying dead trees with a diameter over 7 cm) that remained in the field was about 40 m³ per ha in the salvaged areas and nearly 210 m³ per ha in the localities where the wind-thrown wood was not processed (unsalvaged areas). The status was estimated for the year 2007, i.e., three years after the wind disturbance.

Figure 1. Forested area of the Tatra National Park (TANAP) with the area wind-thrown by the storm in November 2004 (striped) and location of monitoring spots (MSs) in salvaged (black dots) and unsalvaged (white dots) parts.

Table 1. Basic site and tree characteristics of the salvaged and unsalvaged monitoring plots (the High Tatra Mts. in 2019).

Monitoring Plots	Altitude Range (m a.s.l.)	Amount of Deadwood * (m ³ ha ^{−1})	Number of Recorded Trees	Number of Recorded Tree Species **	Mean Lorey's Height (m)
Salvaged	865–1348	209 ± 23	1876	11	4.0
Unsalvaged	853–1388	40 ± 3	1206	6	3.3

* Lying and standing dead trees with a diameter of 7 cm and more [39]. ** Only species with a minimum of 10 individuals recorded at all monitoring plots were considered, specifically: Salvaged plots—common rowan, European larch, goat willow, Norway spruce, Scots pine, silver birch, black alder, common alder, sycamore maple, silver fir and downy birch. Unsalvaged plots—common rowan, European larch, goat willow, Norway spruce, Scots pine and silver birch.

2.2. Tree Measurements

A circular MS was the basic sampling unit of the monitoring system. The centre of each MS was permanently stabilised with an iron tube. The first step of monitoring was to

identify the MS centres in the field based on their coordinates using a GPS device (accuracy of 3–4 m). Then, four circular monitoring plots (MPs), each with a radius of 3 m, were placed around the centre of MSs in the azimuths to the north (0°), east (90°), south (180°) and west (270°) at a horizontal distance between the central point in each MP and the MS centre of 8 m (Figure 2). Hence, 80 MPs representing salvaged and 80 MPs located within unsalvaged areas were included in our survey. Within a single MP, all trees with a height of over 0.1 m were considered for evidence and measurements. Tree species were recorded and a tree height was measured with a wooden ruler with a precision of 1.0 cm. The origin of each tree, i.e., natural regeneration or plantation, was determined. However, since our observation indicated that nearly all trees at the plots (even on salvaged ones) originated from natural regeneration, tree origin was not included as a potential factor in further analyses. At the same time, the growth substrate, specifically soil versus CWD (including lying stems, stumps and root plates) was recorded for each tree. Moreover, damage on trees by game browsing (mostly twig bites) was registered.

Figure 2. Each monitoring spot (MS) with a radius of 8 m consisted of four systematically distributed monitoring plots (MPs).

2.3. Data Processing and Statistical Approach

The measured/recorded tree characteristics (tree species, tree height and occurrence of damage by game browsing) were used to determine the number of trees, number of species, mean tree height and percentage of browsed trees per MP for a set of MPs in salvaged and unsalvaged areas. Tree height was utilised as an independent variable to calculate the aboveground tree biomass using species-specific allometric relationships, which were previously constructed for the conditions of the Western Carpathians (see [40]). A more detailed description of biomass estimation at a plot and territory can be found, for instance, in Konôpka et al. [13]. Here, we wish to explain that two kinds of mean tree heights were calculated for the sets of salvaged MPs and unsalvaged MPs: (i) mean height (as an arithmetic average from all trees) and (ii) Lorey's height (calculated as an average from mean height values of individual MPs). While the first approach does not account for the differences between MPs and considers a set of trees from a salvaged or unsalvaged area as a whole, the second approach is based on average values of all MPs respecting a left-skewed height distribution, which is typical for young forest stands [41].

Data archiving and processing was performed in MS Excel and MS Access and calculations and analyses were performed in MS SQL Server, Visual Studio 2008 and ArcGIS

Desktop. Statistical analyses, including a one-way ANOVA (considering logging and growth substrate aspects) followed by an LSD test ($p < 0.001$) were performed in Statistica 10.0. and R [42]. Results were expressed as average values with standard errors.

3. Results

In total, 3037 trees were recorded and measured at all MPs, while 1834 individuals were found at salvaged MPs and 1203 individuals at unsalvaged MPs. Significantly more tree species were recorded at salvaged than at unsalvaged MPs (F value = 26.57, $p < 0.001$, Table 1). The most frequent species was Norway spruce (1302 recorded individuals), followed by common rowan (643 trees, see Table 2).

Table 2. Tree height characteristics for the salvaged and unsalvaged monitoring plots by tree species (the High Tatra Mts. in 2019).

Tree Species— English (Abbrev.)	Tree Species—Latin Name	Monitoring Plots	Number of Measured Trees	Tree Height Characteristics (m)			
				Mean	SD	Min.	Max.
Common rowan (CR)	<i>Sorbus aucuparia</i>	Salvaged	436	1.9	1.6	0.2	7.5
		Unsalvaged	207	2.3	1.4	0.1	6.0
Goat willow (GW)	<i>Salix caprea</i>	Salvaged	241	2.4	1.7	0.3	7.0
		Unsalvaged	37	2.3	1.8	0.3	6.1
Silver birch (SB)	<i>Betula pendula</i>	Salvaged	321	2.6	2.0	0.2	9.0
		Unsalvaged	38	2.4	1.9	0.2	6.2
Other broadleaves (OB)		Salvaged	161	1.7	1.5	0.3	6.0
		Unsalvaged	5	1.0	0.9	0.4	2.6
European larch (EL)	<i>Larix decidua</i>	Salvaged	147	2.4	1.4	0.2	7.5
		Unsalvaged	49	2.0	1.4	0.2	5.5
Norway spruce (NS)	<i>Picea abies</i>	Salvaged	451	2.0	1.3	0.2	6.0
		Unsalvaged	851	2.1	1.3	0.1	7.0
Scots pine (SP)	<i>Pinus sylvestris</i>	Salvaged	30	2.9	1.4	0.8	5.5
		Unsalvaged	11	1.1	0.8	0.3	3.2
Other coniferous (OC)		Salvaged	47	1.4	1.2	0.2	6.0
		Unsalvaged	5	1.0	0.7	0.3	2.0
All species		Salvaged	1834	2.2	1.6	0.2	9.0
		Unsalvaged	1203	2.1	1.4	0.1	7.0
All species		All	3037	2.2	1.5	0.1	9.0

We found a higher tree density (F value = 5.569, $p = 0.0195$) at salvaged MPs than at unsalvaged ones (25 versus 16 individuals per MP, Figure 3a). Similar results were revealed for the mean number of observed tree species (3.2 vs. 1.9 tree species per MP, Figure 3b) and for the aboveground tree biomass (135 kg vs. 60 kg per MP, Figure 3d). On the other hand, differences in tree height were not significant (F value = 0.355, $p = 0.552$), although trees at salvaged MPs were slightly higher than those at unsalvaged MPs (4.1 m vs. 3.4 m, Figure 3c).

In the next step, tree density was analysed in more detail by dividing MPs into three density groups (Table 3). The results showed that within both groups of MPs, most plots occurred in the least dense group with up to 50 individuals per are (i.e., 102 m², see Table 3). On the other hand, a much higher percentage of salvaged MPs was found in the group with the highest tree density (over 100 trees per are) than of unsalvaged MPs (almost one third versus one seventh of all MPs). Both MP type and tree density influenced tree species composition quantified from tree number (Figure 4a) or aboveground biomass (Figure 4b). As for salvaged MPs, tree density negatively influenced the share of European larch. At unsalvaged MPs, the simplest species composition was found in the density group

with over 100 individuals per are, where common rowan and Norway spruce dominated (Figure 4b).

Figure 3. Comparison of mean number of trees (a), mean number of tree species (b), Lorey's tree height (c) and total aboveground biomass (d) at monitoring plots (MPs) located in salvaged and unsalvaged parts of the area (the High Tatra Mts. in 2019). Differences were tested with an LSD test, which confirmed significant differences in mean number of trees, mean number of tree species and total aboveground biomass (in all cases $p < 0.001$), but not for tree height ($p = 0.552$). Error bars show standard errors.

Table 3. Share of salvaged and unsalvaged monitoring plots grouped with regard to tree density and their average number ($\pm$ standard error; the High Tatra Mts. in 2019).

Density Group (Trees Per Are)	Monitoring Plots	Number of Plots	Share (%)	Average Number of Trees Per Are	Average Tree Height (m)
Below 50	Salvaged	34	42.4	24.1 ± 13.0	2.2 ± 1.0
	Unsalvaged	47	58.7	24.3 ± 13.7	2.2 ± 0.9
51–100	Salvaged	23	28.8	76.7 ± 13.1	2.4 ± 0.9
	Unsalvaged	21	26.3	68.8 ± 11.7	2.2 ± 0.6
Over 100	Salvaged	23	28.8	196.1 ± 70.7	2.3 ± 0.9
	Unsalvaged	12	15.0	183.1 ± 83.0	2.1 ± 0.3
All plots	Salvaged	80	100.0	90.3 ± 82.2	2.3 ± 0.9
	Unsalvaged	80	100.0	60.2 ± 54.9	2.2 ± 0.7

When considering tree species composition for all salvaged and unsalvaged MPs, clear differences between two types of MP were found. Contribution of spruce at unsalvaged MP was more than twofold of its share at salvaged MP (Figure 4a,b). Rowan had a very similar contribution at both types of MP (25% or 16% and 22% or 17% at salvaged and unsalvaged MPs calculated from the number of trees or biomass, respectively). All other species had higher shares at salvaged than at unsalvaged plots. Although the results for tree species composition quantified from the number of trees or aboveground tree biomass were rather similar (compare Figure 4a,b), biomass shares showed a slight dominance of

birch (28%) over Norway spruce (23%) at salvaged MPs due to the greater dimensions of birch trees (Table 2).

Game damage was found to have a significant impact on the number of trees per MP (F value = 12.35, $p < 0.001$), number of species per plot (F value = 19.9, $p < 0.001$) and mean tree height (F value = 13.74, $p < 0.001$). Moreover, information from the field survey at MPs confirmed a great influence of post-disturbance management on the frequency of game browsing on trees. The percentage of browsed trees at salvaged MPs was more than twofold of that at unsalvaged MPs (Figure 5a). Our results showed that while the game browsing of Common rowan was frequent (Figure 5c), that of Norway spruce was negligible (Figure 5b). While the browsing percentage of European spruce was similar at both types of plots (1.3% and 0.8% at salvaged MPs and unsalvaged MPs, respectively), contrasting results were recorded for rowan (64% at salvaged MPs and 30% at unsalvaged MPs).

Figure 4. Mean tree species composition at salvaged and unsalvaged plots quantified from number of trees (a) and aboveground biomass (b) in three classes of tree densities (less than 50 individuals per are, 51 to 100 individuals per are, more than 100 individuals per are, the High Tatra Mts. in 2019). See Table 2 for explanation of tree species abbreviations.

Figure 5. Share of browsed trees at salvaged and unsalvaged monitoring plots (MPs) for all tree species together (a), Norway spruce (b) and common rowan (c); the High Tatra Mts. in 2019. Differences between salvaged and unsalvaged MPs were tested with an LSD test. Significant differences were confirmed for all species and common rowan (in both cases $p < 0.001$), but not for Norway spruce ($p = 0.628$). Error bars show standard errors.

From the point of view of growth substrate, our survey showed much higher, approximately fivefold share of trees on CWD at unsalvaged than at salvaged MPs (Figure 6a for the number of trees and Figure 6b for the tree aboveground biomass). However, the share of trees growing on CWD was rather low even at unsalvaged MPs (about 15% and 9% of number of trees and aboveground tree biomass, respectively).

Figure 6. Share of trees growing on coarse woody debris (CWD) at salvaged and unsalvaged plots expressed from the number of trees (a) and aboveground biomass (b) (the High Tatra Mts. in 2019). Differences were tested with an LSD test, which confirmed significant results in both cases ($p < 0.001$). Error bars show standard errors.

Finally, our interest focused on differences in tree size between individuals growing on soil and CWD. For this analysis, all trees measured at salvaged and unsalvaged MPs were included. The differences between the growth substrate were significant for both tree height (F value = 16.20, $p < 0.001$) and aboveground biomass (F value = 14.57, $p < 0.001$). Specifically, trees growing on soil were taller (Figure 7a) and had nearly twice as much aboveground biomass (Figure 7b) as those found on CWD.

Figure 7. Mean height (a) and mean aboveground biomass per tree (b) for individuals growing on two different substrates, i.e., soil versus coarse woody debris (CWD)—results for salvaged and unsalvaged plots together (the High Tatra Mts. in 2019). Differences were tested with an LSD test and showed significant differences for tree height ($p < 0.001$) as well as for aboveground biomass ($p < 0.001$). Error bars show standard errors.

4. Discussion

Our survey, performed in the TANAP, revealed higher tree density, greater tree species richness and higher biomass production in the areas from which the wind-thrown wood was extracted than in those left to self-development without calamity wood logging (Tables 1–3). In addition, more evident dominance of spruce was recorded at unsalvaged than salvaged plots. At both types of plots, common rowan was another frequent tree species besides Norway spruce (Table 2, Figure 4). The main difference between the two types of plot was that birch was much more frequent at salvaged plots (Table 2, Figure 4). We supposed that the differences between salvaged and unsalvaged sites would be primarily related to the contrasting amount of CWD due to wood removal from managed sites,

which subsequently affected micro-climatic (especially temperature and moisture) conditions at or near the ground surface and in the upper soil. Several works (e.g., [23,26,43]) concluded that CWD can be an effective substrate for tree regeneration of spruce, particularly in mountainous regions. Mai [44] even reported that at altitudes above 1400 m a.s.l. CWD is the basic form of spruce seedbed. Another study [30] performed in the High Tatra Mts. indicated that wood processing supported tree species diversity due to the disruption of ground surfaces that had already been colonised by spruce saplings, and thus created space for other tree species. Similarly, a field survey from southwestern Pennsylvania, USA [19] showed that post-windthrow salvage logging increased seedling diversity a few years after the wood removal with little impact on species composition.

Our analyses of tree species composition in three tree density classes (up to 50, 51–100 and over 100 trees per are) did not show very clear tendencies with density (Figure 4). Perhaps the only exception is the decreasing share of larch with increasing tree density at salvaged plots. This may be linked to its light-demanding character [45]. However, this trend was not revealed for other light-demanding tree species, such as birch, rowan or willow. We assume that this is probably because they are fast-growing species, and light was not the factor limiting their successful regeneration after the large-scale wind disturbance in 2004. A study on natural regeneration performed in Canada showed that a lack of suitable substrate may be the main barrier to regeneration establishment [46].

The least diverse tree species composition with a huge dominance of Norway spruce and common rowan was observed at the densest unsalvaged plots. We assume that these two species were very successful in colonising the disturbed area and created very dense clusters. These did not allow other species (especially light-demanding ones, such as pine or larch) to regenerate or survive at the same microsites. The different situation observed at salvaged plots might be related to the destruction of these early growth stages of dominant tree species by wood logging and thus freeing space for other species (see also [30]).

Game browsing (under the conditions of the High Tatra Mts., especially red deer browsing) frequency was significantly different between salvaged and unsalvaged plots. Much more frequent browsing at salvaged plots in comparison to unsalvaged ones might be related to more frequent obstacles in the form of lying windthrown wood in unsalvaged parts. For instance, restricted movement of red deer due to lying logs and subsequent decreased browsing was identified as a reason for the occurrence of rowan seedlings in the southern part of Poland [29]. A similar positive effect of deadwood occurrence on silver fir saplings in areas over-abundant in roe deer was proven in southern Germany [47].

Excessive game pressure usually leads to a decreased diversity in a young tree generation [48], which was, however, not documented in our results, as the more diverse tree species composition was observed in the more browsed salvaged part (Figure 5). There may be two possible explanations for this result. One is related to game density, which was found to have an adverse effect on the diversity of subsequent forest stands only if it exceeds the carrying capacity of the area [49,50]. In contrast, moderately browsed areas were found to have the highest species richness, because game pressure regulated inter-tree competition [49,50]. The other explanation is linked to the specific tree species that deer damage, tree species abundance and its susceptibility to damage [50–52]. Browsing of infrequent admixed tree species can reduce the overall tree species diversity and sometimes may even result in species loss [53], while damaging the most abundant tree species in regeneration by game may have a positive effect on tree species diversity [51,54].

Tree susceptibility to damage also affects the final state of the subsequent forest stand. For example, many papers from Europe have shown that common rowan is extremely prone to browsing (e.g., [55–57]). Extremely frequent damage on rowan in comparison to spruce (Figure 5) could be related to deer foraging preferences for more palatable species, which consequently loosens forage pressure on less attractive species (e.g., [58,59]).

The share of trees growing on CWD at unsalvaged plots was approximately fivefold of the share observed at salvaged plots. This difference is in accordance with the findings on the amount of lying wood, the estimates of which were five times greater in unsalvaged

than in salvaged areas (specifically 210 versus 40 m³ per ha, see [39]). However, our results indicated a rather low share of trees growing on CWD even at unsalvaged sites in comparison to other works from mountainous old-growth forests. For example, Vorčák et al. [22,23] reported that, at the Babia hora mountain, more than half of spruce regeneration occurred on CWD, while in our study it was less than 15% of all recorded individuals. The reason for this apparent discrepancy is the stage of wood decay. The surface of rather fresh wood is not suitable for tree seed germination and development of saplings and seedlings [22,26] because it is too hard to penetrate. Wood needs to be at least partly decomposed to serve as a seedbed. For instance, Orman and Szewczyk [26] studied growth and density of Norway spruce saplings and seedlings on CWD regarding its decay classes (from the 1st—least decomposed to the 5th—most decomposed). Optimum growing conditions on CWD were found in the 4th class, while nearly no young trees grew on CWD in the 1st class. Similar results were reported by other works (e.g., [22,60]).

In our case, the essential part of CWD originated from the windstorm in November 2004. This means that, in the season of our field measurements, the CWD was nearly 15 years “old”. According to Harmon and Franklin [61], within the first 15 years of CWD existence, logs are usually colonised by bryophytes, while tree regeneration tends to occur on logs older than 15 years. However, the actual timing of seedling establishment depends on the actual conditions provided by the CWD. Moss layers, holes or crevices in wood provide suitable substrates for seed germination [61–63]. Decaying wood decreases its density [64], the wood becomes softer and thus easier to penetrate [65]. According to Holeksa [66], decomposition of spruce logs in similar mountainous conditions as in the High Tatra Mts. may take up to 150 years, while the stage suitable for the establishment of regeneration is usually reached only after 35 or more years. At the time of our field measurements, lying wood and stumps were not intensively decomposed. We estimated that the prevailing portion of dead wood might have hardly reached the third, i.e., the middle decay class according to [26]. It means that CWD has very probably not reached optimum conditions for forest regeneration yet.

Furthermore we found that trees on CWD were smaller than those growing on the soil ground. This may result from the delay in forest regeneration establishment on CWD in comparison with the trees growing on soil rather than from contrasting growth rates. Previous research [26] had shown that trees growing on CWD had a slightly faster height increment than those on soil. However, the mentioned study examined trees on CWD in all decay classes. Thus, this mild advance may not be characteristic for every stage of wood decomposition.

Finally, we wish to point out that although forest cover at salvaged areas was more developed and richer in tree species composition than at unsalvaged areas, the results must be considered with regard to the temporal scale the data covered. The situation was observed in young, about 15-year-old forests. However, trees often live for over 100 years, and in the areas with a high level of nature conservation even a couple of hundred years, during which tree species composition and forest structure change over time. Many previous papers (e.g., [31,67–69]) highlighted positive effects of dead wood on flora and fauna biodiversity or even claimed dead wood as an important factor in the mitigation of forest degradation [70].

On the other hand, wood is still the main product (renewable source) of commercial forests, which is usually obtained thanks to forestry activities, i.e., invested work and finances. Hence, wood represents income for forest stakeholders and is also needed for industry and finally for human use in quotidian life. Considering ongoing climate change, we may expect that the logging of calamity wood will remain (if not increase its share) an important part of forest harvesting in future. The proportion between managed and unmanaged post-disturbance areas would still be regulated by forest categories from the perspective of its main purpose (commercial versus nature conservation). Especially in national parks, dividing forest areas into specific levels of nature protection, which would specify principles for forest management (including post-disaster measures), can mitigate

potential conflicts between foresters and conservationists. We are convinced that, in general, not only should two kinds of opposite forest management types, i.e., strictly commercial and fully protected (i.e., absolutely no management), be promoted. Contrariwise, a broad range of different management intensities and a variety of dead wood amounts left on site should be applied with respect to local conditions. We assume that this kind of diversified post-disturbance management would promote principles of sustainability [15], leading to parallel fulfilment of multiple ecosystem services and biodiversity [71].

5. Conclusions

The results from the High Tatra Mts. showed contrasting properties of young forests located in salvaged and unsalvaged areas 15 years after the large wind disaster. Rather surprisingly, the current status was in favour of salvaged areas (from which calamity wood was logged), since the young forests there were composed of more tree species, and accumulated more biomass than those in the unsalvaged area. This situation occurred in spite of higher browsing intensity in the salvaged areas. The main findings could lead to two contradictory conclusions. The positive one is that the spatially differentiated post-disturbance management of a certain area can combine both forestry and nature conservation interests. At the same time, this approach can generate different types of forests with contrasting properties that might positively influence future forest stability. Consequently, windstorm or bark beetles, which usually follow wind disturbances in spruce forests, would not destroy the whole area at the same time. The synergetic negative effects of wind destruction and bark beetle infestation often occur when unlogged wind-thrown wood creates favourable conditions for bark beetle outbreaks. Consequently, bark beetles can destroy forests covering even larger areas than those destroyed by wind itself. Thus, co-occurring different types of forests in one region can mitigate these kind of “chain” processes. On the other hand, a negative side of such a contrasting management is that it can cause an uneven distribution of red deer population and intensive browsing of trees growing at areas favourable for game life and feeding.

Our research covered a relatively short period of forest development. To obtain more information, this kind of a comparative study should be performed over a longer time. In perspective, only long-term field observations can bring more relevant knowledge on impacts of post-disturbance management to forest development in various growth stages. Comprehensive findings on optimal post-disturbance management would create a theoretical base for setting up sustainability of forest cover under changing, especially climatic conditions and its inherent phenomena (windstorms, forest fires, drought, pests, etc.).

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