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Source: Mountain Research and Development, 39(1)

Published By: International Mountain Society

URL: <https://doi.org/10.1659/MRD-JOURNAL-D-19-00008.1>

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Species Composition and Carbon Stock of Tree Cover at a Postdisturbance Area in Tatra National Park, Western Carpathians

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Our study focused on a postdisturbance area that arose after the large-scale windstorm on 19 November 2004 in Tatra National Park, northern Slovakia. The wind destroyed forest stands dominated by Norway

spruce at elevations from 700 to 1400 m above sea level. The windstorm dramatically changed the forest stands in the national park, motivating our research teams to study postdisturbance tree cover dynamics. We quantified tree species composition (diversity) and carbon pool in whole-tree biomass of young forest stands after the disturbance, in 2007, 2010, and 2016. The number of tree species was significantly greater at lower (below 900 m; foothill sites) than higher elevations (above 900 m; mountain sites). The number of species increased between 2007 and 2010, and after 2010 almost stabilized. In 2007, estimates showed an average of 1.9

tons of carbon per hectare in the lower sites and only 0.4 tons in higher sites. Between 2007 and 2016, carbon stocks in whole-tree biomass grew to 11.5 t ha^{-1} in lower sites and 5.3 t ha^{-1} in higher ones, with an average for the entire area of about 8 t ha^{-1} . Estimates showed that the carbon stock in whole-tree biomass before the calamity (in 1996) was 101 t ha^{-1} . After the wind disturbance, higher biomass stock was found among conifers (especially Norway spruce) at lower elevations and among broadleaves (mostly birch) at higher elevations. We found that tree species composition after the wind disturbance was more diverse than that before forest destruction. The current tree species composition seems to be a positive consequence of disturbance, especially given the species composition's resistance to harmful agents, including wind and bark beetles.

Keywords: Disturbance; wind damage; whole-tree biomass; carbon stock; young forest; Slovakia.

Peer-reviewed: December 2018 **Accepted:** March 2019

Introduction

Ongoing climate change and the increasing frequency of large-scale forest disturbances in Europe disrupt the continuity of forest cover and their ecosystem functions (Fleischer et al 2017). Research has shown that large-scale disasters (wind, fire, bark beetles, etc) in forests cause huge carbon losses in both tree biomass and soils (Seidl et al 2014). On the other hand, the effects of forest disturbances on the diversity of fauna and flora, including tree species, are less clear and might manifest themselves in opposite manners (Ilison et al 2007; Allen et al 2012). Thom and Seidl (2016) indicated that while forest disturbances affect mainly provisioning ecosystem services, their effects on biodiversity have often been positive ("disturbance paradox"). However, carbon loss caused by disturbances is predicted to increase uncontrollably in forest ecosystems, leading to an undesired increase of CO_2 in the atmosphere (Seidl et al

2014). Another recent threat from disturbances relates to decreasing biodiversity, which negatively influences most ecosystem services (Harrison et al 2014). Biodiversity degradation has a major impact on ecosystem functioning and secondarily on human welfare (Díaz et al 2018).

Long-term records in Slovakia show that large-scale disturbances in forests have increased, especially in the last 2 decades (Kunca et al 2019). At the same time, the records show that windstorms have been the most destructive disturbance in nearly all years of observation. In Slovakia, the largest wind disturbance since 2000 (windstorm Elisabeth) occurred in November 2004 (Konôpka, Zach, et al 2016). The wind hit the northern and central parts of the country particularly hard, with the epicenter of forest destruction in the High Tatra Mountains and Podtatranská Basin, which mostly belong to the Tatra National Park (TANAP). Before the disturbance, mature forests covered most of the area, with the majority of trees aged between 61 and 120 years

(Konôpka, Pajtk, et al 2016). The forests were mostly Norway spruce (*Picea abies* L. Karst), which, by the close of the 20th century, represented nearly 80% of the wood stock in the region (Vološuk et al 1994). Mature spruce stands in Slovakia are very prone to wind damage because of the shallow root system, a relatively low resistance of the wood to breaking, and the large, wind-catching vertical profile of the crown area (Konôpka, Zach, et al 2016).

Throughout the 20th century, wind disturbances occurred repeatedly in the TANAP in 1915, 1925, 1941, 1964, 1968, 1981, and 2002 (only those with a volume of damaged trees over 100,000 m³ are listed; Koreň 2005). Damage to forests caused by windstorms may not always have large-scale impacts. For instance, between 1977 and 1997, wind damage affected areas up to 0.5 ha in the TANAP (Fleischer 1999) in 80% of cases. Destroyed areas usually supported the rapid growth of pioneer soft-broadleaved tree species. Under their protection, climax coniferous species, such as Norway spruce (*Picea abies*), European larch (*Larix decidua*), Scots pine (*Pinus sylvestris*), and—more rarely—silver fir (*Abies alba*) gradually took hold. A special case of forest development occurs in the central part of the High Tatra Mountains. In so-called successional forests (ie tree species composition where the horizontal and vertical structure has not yet reached a climax stage), Norway spruce, European larch, and Scots pine appear abundantly, but the forests do not reach climax stage because of destruction caused by *bora*-like windstorms (Koreň 2005).

To determine the actual carbon balance in forested land and to quantify the gradual decrease of carbon stock accumulation in whole-tree biomass after extensive disturbances, estimates of all tree components (foliage, branches, stem, roots) in newly established (young) stands are necessary. Biomass and the resulting amount of carbon in these stands are usually calculated using mathematical models with allometric relationships (West 2009). These allometric relationships generally describe the amount of tree biomass (or its component) depending on easily measurable characteristics, typically stem diameter and/or tree height. During the last 2 to 3 decades, European scientific groups (eg Zianis et al 2005; Skovsgaard et al 2011; Krezja et al 2017) have developed national or transnational mathematical models for the most important forest tree species in the region. However, almost all studies have focused on the construction of models for trees with a stem diameter above 7 cm (Wirth et al 2004). Recently, we began constructing allometric relationships for small trees from 12 main species (Pajtk et al 2008, 2011, 2018); our results enabled us to calculate the amount of whole-tree biomass in most types of species mixtures at young stages of growth in the territory of Slovakia (Konôpka et al 2013). The present paper aims to address the lack of knowledge about carbon stock fixed in developing young stands after the historically largest wind

damage event in Slovakia's oldest national park, using our previously constructed allometric relationships.

We quantified tree species composition (diversity) and carbon stock in whole-tree biomass of young forest stands that grew after the large-scale wind disturbance in the TANAP. We focused on the effects of temporal and elevational aspects of these forest characteristics, by comparing results 3, 6, and 12 years after the windstorm episode, and distinguishing between effects in the foothill zone (up to 900 m above sea level [asl]) and the mountain zone (above 900 m asl). Finally, we described tree species compositions and carbon stocks in whole-tree biomass, comparing results before and after the wind disturbance.

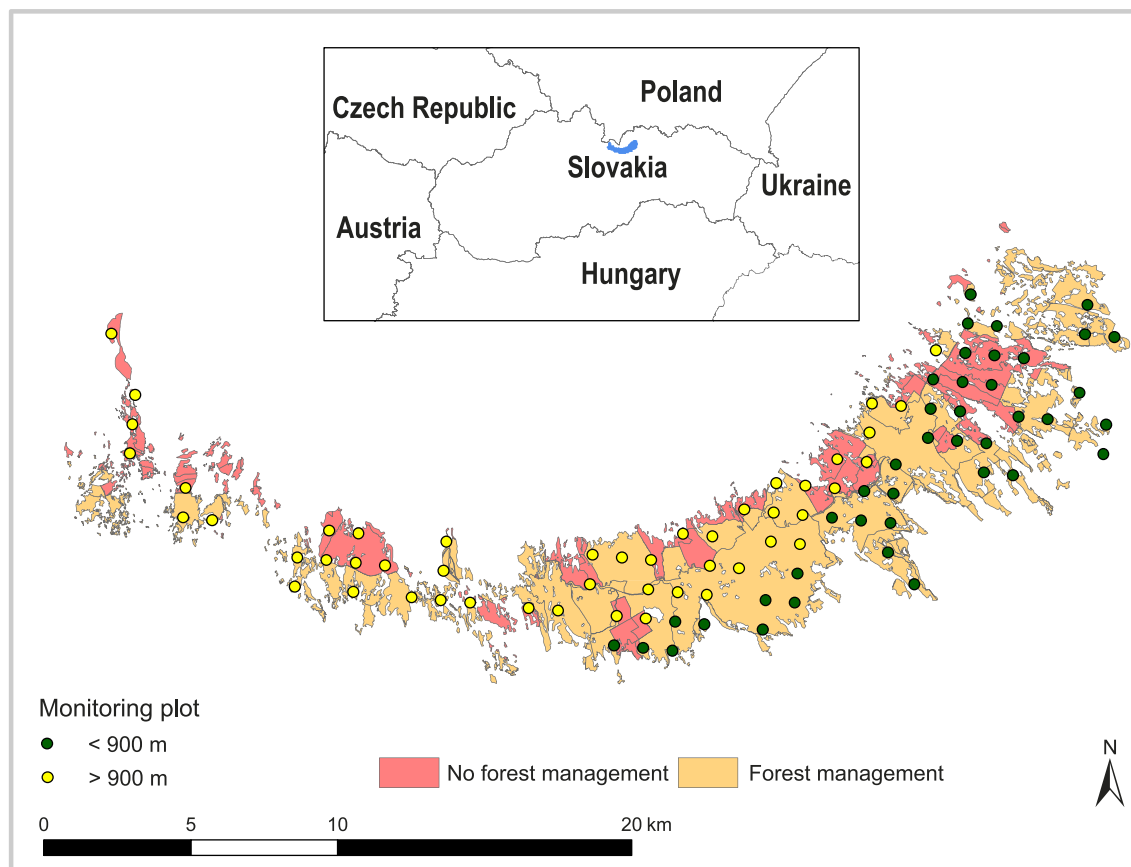
Study area

Our study focused on the High Tatra Mountains, in northern Slovakia. Here, the bedrock is predominantly formed by sediments of granodiorites. Forest soils are mostly lithic Leptosols and Podzols. The climate is typically cold (annual mean temperature is about 5.0°C) and moist (annual total precipitation over 1000 mm), with snow cover lasting between 110 and 130 days (Konček 1974).

On 19 November 2004, a large-scale windstorm damaged parts of the TANAP—the largest and oldest protected area in Slovakia. The wind destroyed forest complexes dominated by Norway spruce at elevations from 700 to 1400 m asl. The disturbance area was concentrated in a continual belt 35 km long, oriented in a west–east direction (Šebeň 2011a). The forest stands in this belt were almost entirely destroyed (mainly uprooted, with some stem-broken), except for a few forest clusters with a preponderance of European larch and, on a few sites, Scots pine. The area of the damaged forests covered approximately 12,600 ha (Koreň 2005).

The postdisturbance area was managed in 3 different ways related to the degree of conservation that was targeted: (1) processing of all merchantable wood followed by reforestation, mostly through tree planting, (2) partial processing of calamity wood (30–60% of merchantable wood) with reforestation in the form of a combined approach: mostly natural regeneration but also some planting, and (3) exclusion of wood processing and letting natural succession take place. The main part of the calamity wood was processed within 2 years of the disturbance (2005–2006). As for forest regeneration, different approaches were implemented depending on the level of conservation targeted (Figure 1). A few years after the disturbance (from 2006 to 2010), nearly half of the area was replanted with European larch, Norway spruce, Scots pine, sycamore (*Acer pseudoplatanus*), and silver fir (Marhefka 2015). Preliminary results from the monitoring of the revitalization processes in the TANAP (situation in 2007–2008) indicated that natural and

FIGURE 1 Location of the windthrow belt in Central Europe, and core of the windthrow area in the Tatra National Park, showing the monitoring plots in 2 zones (foothill, $n = 41$, and mountain, $n = 49$), and high-level and low-level nature conservation areas. (Map by Vladimír Šebeň)



combined reforestation prominently prevailed over purely planted stands (Šebeň 2011a).

Material and methods

Estimation of predisturbance whole-tree biomass and species composition

The carbon stock in whole-tree forest biomass at the study area was calculated using data from the Forest Management Plan (FMP), created in 1996. Thus, this calculation characterizes the situation 8 years before the wind disturbance. A database of stand characteristics processed in MS Access and FoxPro was used. Subsequently, ArcMap was used for identification and visualization of forest stand borders that belonged to the analyzed postdisturbance area.

From the FMP database, the following stand characteristics were used as input data for further calculation:

- Mean stem diameter (cm);
- Mean tree height (m);
- Number of trees per hectare;
- Contribution of each species to stand basal area (%);
- Total stand area (ha).

First, the stem volume of the mean tree in a specific stand was calculated by using diameter at breast height (thickness of stem measured 130 cm from the ground level) and tree height as predictors (Petráš and Pajčík 1991). Then, the stem volume in individual species was multiplied by the number of trees per hectare and total stand area. The sum of stem volumes in all species was converted to weight of dry mass (biomass) using stem wood density (Požgaj et al 1993). Hence, the amount of total stem biomass for each tree species per stand was obtained. To assess the biomass of other tree components (foliage, branches, stump, and roots), the biomass of the mean tree in each species was calculated using regression equations where breast height diameter and tree height were predictors. Foliage, branch, stump, and root biomass of the mean tree was multiplied by the number of trees per hectare and the stand area. Total biomass stock (whole-tree biomass) per stand was expressed as the sum of all tree components (stem over bark, foliage, branches, stump, and roots) in all tree species together. Finally, carbon stock per stand was calculated as 50% (Matthews 1993) of total whole-tree biomass. The detailed calculation procedure and the equations originating from other authors are described in Pajčík et al (2009).

TABLE 1 Coefficients (b_0 , b_1) and correction factors (λ) for allometric equations expressing whole-tree biomass based on tree height as an independent variable.

Tree species	b_0	b_1	λ	Reference
Birches ^{a)}	3.711	2.591	1.181	Own unpublished data
European larch	4.840	2.559	1.237	Pajtík et al (2018)
Goat willow	3.589	2.879	1.104	Pajtík et al (2018)
Norway spruce	5.304	2.239	1.157	Pajtík et al (2008)
Rowan	3.522	3.104	1.125	Pajtík et al (2018)
Scots pine	5.013	2.104	1.209	Pajtík et al (2011)

^{a)} Especially *Betula pendula* and *Betula pubescens*.

Estimation of postdisturbance whole-tree biomass and species composition

Species composition, tree density, and whole-tree biomass (carbon) stock in young forest stands in the postdisturbance area were estimated based on 90 monitoring plots (MP) established in a 1 × 1 km grid (Figure 1). In each MP, 4 circular plots (satellite subplots, or SSP) located 8 m away from the center to the cardinal north, east, south, and west were established to record trees. Each SSP had a radius of 3 m. The species and height of trees were recorded with a precision of 10 cm, covering all individuals from a height of 0.1 m on a total of 360 subplots distributed across the whole postdisturbance area. The measurements were captured during the 2007, 2010, and 2016 growing seasons.

Biomass quantity per tree was calculated using species-specific allometric relations for birches (*Betula* spp.), European larch, Norway spruce, goat willow (*Salix caprea*), rowan (*Sorbus aucuparia*), and Scots pine. Tree height was used in allometric relations as an independent variable (Konôpka, Zach, et al 2016), applying the following equation:

$$W = e^{(b_0 + b_1 \cdot \ln h)} \lambda,$$

where W represents whole-tree biomass (ie weight of all components: foliage, branches, stem, and roots, in kg), b_0 and b_1 are equation coefficients (see Table 1; unitless), h is tree height as an independent variable, in m, and λ is the transformation correction factor (see Table 1; unitless).

The category “other coniferous tree species” was calculated according to the model derived for Scots pine, and “other deciduous tree species” was calculated according to the goat willow. The amount of carbon fixed in the tree biomass was calculated using a standard coefficient equaling the value of 50%.

For each SSP, the number of tree species, the number of tree individuals, and the whole-tree biomass (carbon) stock per specific species were calculated. Subsequently, these characteristics were expressed at the MP level as the average numbers from 4 SSPs. While the numbers of tree species were expressed at MP level (ie microsite scale), the

number of trees and the carbon stock in whole-tree biomass were upscaled to hectare level.

Statistical analyses

Data archiving and manipulation were performed using MS Excel and MS Access, calculations and analyses were done with an MS SQL Server, Visual Studio 2008, and ArcGIS Desktop; visualizations were done in ArcMap. Statistical analyses were performed using Statistica 10.0., including a two-way analysis of variance (ANOVA; considering both spatial and temporal aspects) followed by Fisher’s Least Significant Difference (LSD) tests ($p < 0.05$). Results were expressed as average values \pm standard errors.

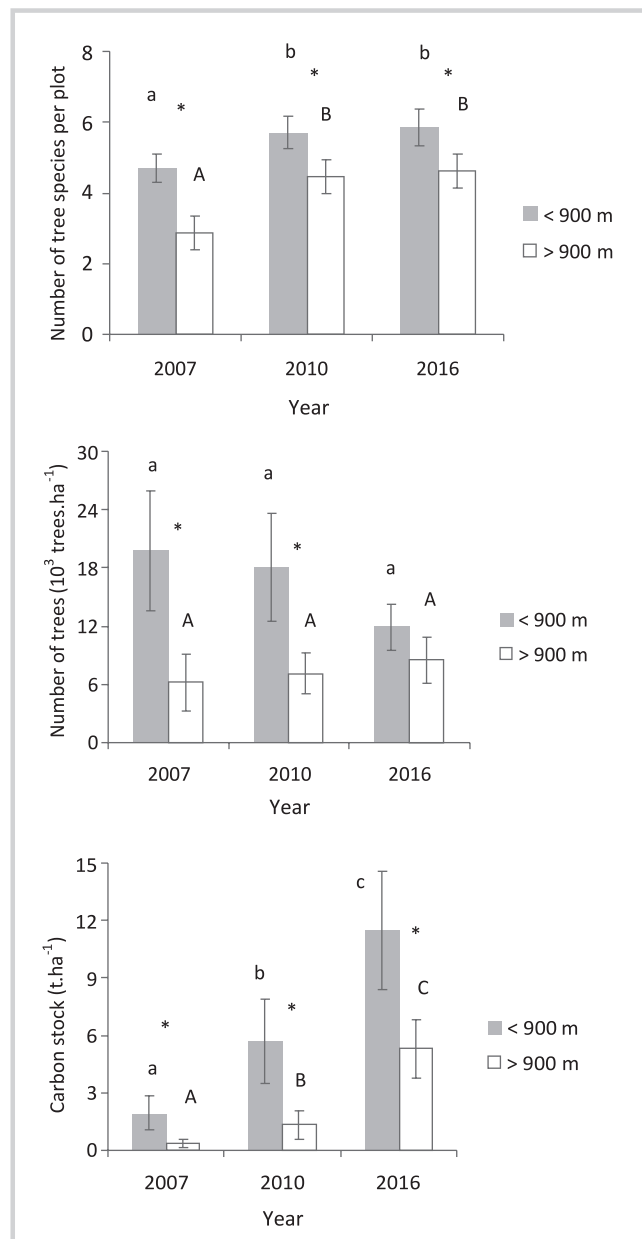
Results

The number of tree species was significantly higher on MPs at lower elevations (ie up to 900 m) than at higher elevations (above 900 m) (Figure 2, top). The number of species grew between 2007 and 2010 and then nearly stabilized. Specifically, the average number of species at the lower sites was 4.7, and the average number of species at the higher sites was 2.9 in 2007; by 2016, these values were 5.9 and 4.6, respectively. Note that the number of forest tree species expresses a sort of mean situation at a microsite level and does not represent the postdisturbance area as a whole.

Larger elevational differences than in the case of the number of species were found for the number of individuals per hectare (Figure 2, middle). In 2007, there were almost 20,000 trees per hectare at lower elevations, but at higher elevations, the number was just slightly over 6000. These elevational differences diminished as the years went by. Interestingly, while the number of individuals declined steadily in the lower MPs, likely as a result of competition among trees, a slight increase was found in the higher sites.

Further contrasts between the sites in the foothill and mountain zones were found: The most significant differences were recorded in the whole-tree carbon stock

FIGURE 2 Mean number of tree species per microsite (top), mean number of trees per hectare (middle), and mean whole-tree carbon stock per hectare (bottom) recorded in the monitoring plots. Significant differences between the specific years are indicated by a, b, c for elevations below 900 m, and by A, B, C for elevations above 900 m. Asterisks show significant differences between sites below and above 900 m in each year. Statistically significant differences ($p < 0.05$): vertical lines indicate \pm double values of standard errors (ie 95% confidence intervals).



(Figure 2, bottom). Specifically in 2007, an average of 1.9 tons of carbon per hectare was quantified for sites below 900 m, with only 0.4 t ha $^{-1}$ for sites above 900 m. After 2007, the carbon stock in whole-tree biomass increased significantly, so that by 2016, the average carbon pool was 11.5 t ha $^{-1}$ at elevations below 900 m and 5.3 t ha $^{-1}$ in the areas situated above 900 m.

Our results also provide quantification of the share of individual species (or group of species) (Figure 3) to the carbon pool in whole-tree biomass. Significant differences were found regarding both elevation (below 900 m and above 900 m) and time (years 2007, 2010, and 2016). While

coniferous trees prevailed on the sites below 900 m, the opposite was found in areas above 900 m, dominated by broadleaved trees. The temporal comparison (2007, 2010, and 2016) showed a decline in the contributions of spruce and rowan to carbon stock and an increase for the share of birch. When comparing the share of species to the number of trees and to the carbon pool (see Figure 3 versus Figure 4), evident differences were detected. For example, the share of spruce to the number of individuals was half of its share to the carbon stock in the lower sites. This suggests that spruce at lower elevations represented more biomass per individual tree in comparison with other species.

The carbon stock in whole-tree biomass grew during the years measured in all species (Tables 2 and 3). Rowan was the only exception recorded, with biomass stagnation at elevations below 900 m. In 2016, per hectare carbon stocks in the MPs located at sites below 900 m for specific tree species were as follows (from the largest to the smallest values): Norway spruce: 5.4 t; birches: 2.82 t; other broadleaves: 1.4 t; Scots pine: 0.6 t; European larch: 0.5 t; goat willow: 0.3 t; and other conifers: 0.2 t. In the MPs located above 900 m, per hectare carbon stocks were: Norway spruce: 1.8 t; birches: 1.4 t; rowan: 0.8 t; European larch: 0.5 t; goat willow: 0.5; Scots pine: 0.2; other conifers: 0.1 t.

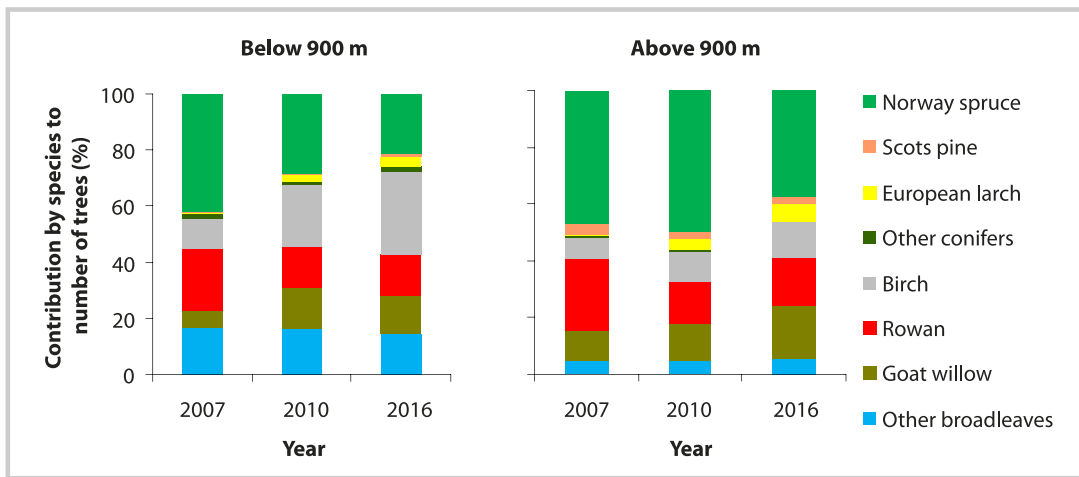
Our results suggest that while average carbon stock in whole-tree biomass before the wind disturbance (year 1996) was 101 t per hectare, at 12 years after the disturbance, it was only about 8 t per hectare. In 1996, most of the stands (nearly 70%) contained per hectare carbon stock over 40 t, but by 2016, only two MPs (2%) had carbon stock equaling only slightly over 40 t (Figure 5). A further contrast between the statuses in 1996 and 2016 was found in tree species composition (Figure 6). In 1996, as much as 98% of all tree carbon was fixed by 3 main coniferous species: spruce, pine, and larch. In 2016, these coniferous species contributed only 53%. The largest increase in carbon stock share between 1996 and 2016 was found for birches (from 0.5% to 25%). While other coniferous species remained at nearly the same share (about 1.5%), evident increases were found for rowan, goat willow, and especially other broadleaved species.

Discussion

Tree species composition

Significant differences in the tree species compositions (and corresponding whole-tree biomass base) were observed between the lower and higher sites. Specifically in the mountain zone, broadleaved species (mostly birch) dominated, while the foothill zone showed prevalence of conifers (mostly spruce). This situation is mainly due to the ecological requirements of trees at the initial growth stage (Kuijk et al 2014). These differences between sites at different elevations may also be partly related to postdisturbance management. In principle, a greater

FIGURE 3 Contribution of tree species to number of trees in the locations below and above 900 m.



proportion of artificial reforestation can be assumed at lower elevations than at higher ones, due to accessibility for planting as well as differences in degrees of nature conservation.

Comparison of forest composition before and after the disturbance revealed a postdisturbance increase in tree species diversity. Previous studies have identified this phenomenon in a variety of ecosystems (eg Wilkinson 1999; Thom and Seidl 2016). However, a meta-analysis revealed frequently conflicting or insignificant patterns (Mackey and Currie 2001). Theoretically, the consequences of disturbances on species diversity in ecosystems are usually related to the extent of disasters: Typically, small-sized disturbances have more positive impacts than larger ones (Dornelas 2010).

Another important factor influencing the species diversity of forest stands is the length of time after the disturbance episode (Ilison et al 2007). In our case, an increase in the average number of species on the microsites was observed between the third year and

seventh year after the disturbance. Subsequently, the number of species stabilized. We expect no further increase in tree species diversity in future; on the contrary, we predict that the abundance of some trees species, goat willow and rowan in particular, will be reduced by intensive deer browsing (Pajtík et al 2015). In the long term, more than 50 years, we may expect a reduction in the share of short-lived trees species, namely birch, rowan, goat willow, and perhaps other broadleaved species. By contrast, long-lived species will form a substantial part of old stands in future (Kacálek et al 2017). However, we believe that the High Tatra Mountains are among the areas in the Carpathian arch most threatened by climate change (Melo et al 2013). Therefore, the survival of Norway spruce in the forests of the High Tatra Mountains is rather crucial in long-term postdisturbance regeneration (Hlásny et al 2017; Kruhlov et al 2018). European larch is also vulnerable to changing climate conditions in the long term (Danek et al 2017). Positive selection of tree populations with high resistance

FIGURE 4 Contribution of tree species to carbon stock in the whole-tree biomass in the locations below and above 900 m.

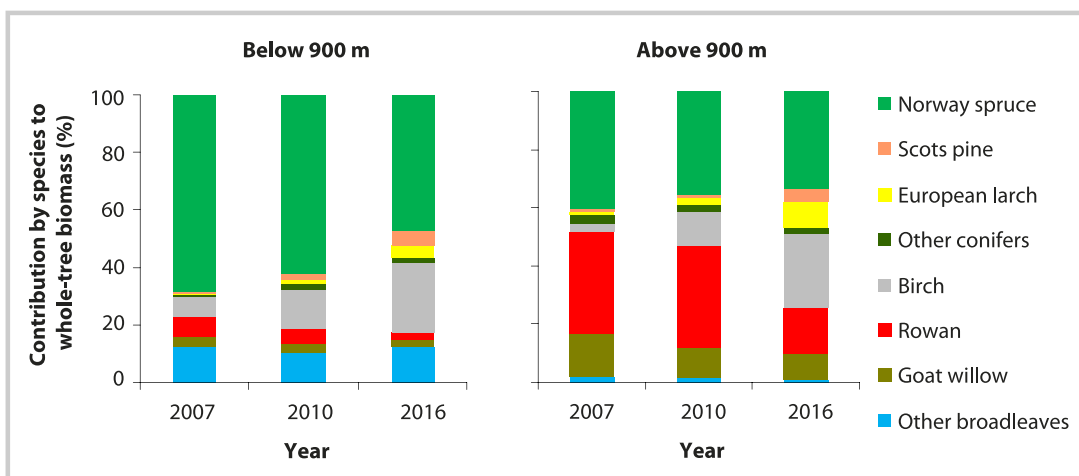


TABLE 2 Carbon stock in the whole-tree biomass of the different coniferous species according to years measured and elevational zones (mean values \pm double values of standard errors, ie 95% confidence intervals).

Coniferous species	Elevational zone (m above sea level)	Carbon stock per year (t ha^{-1})		
		2007	2010	2016
Norway spruce	Below 900	1.32 \pm 0.84	3.54 \pm 2.00	5.40 \pm 1.98
	Above 900	0.15 \pm 0.10	0.47 \pm 0.46	1.77 \pm 0.66
Scots pine	Below 900	0.02 \pm 0.03	0.11 \pm 0.11	0.61 \pm 0.63
	Above 900	0.01 \pm 0.01	0.01 \pm 0.02	0.23 \pm 0.23
European larch	Below 900	0.01 \pm 0.03	0.09 \pm 0.14	0.49 \pm 0.36
	Above 900	0.01 \pm 0.01	0.03 \pm 0.03	0.48 \pm 0.24
Others	Below 900	0.01 \pm 0.02	0.10 \pm 0.38	0.18 \pm 0.20
	Above 900	0.01 \pm 0.07	0.03 \pm 0.18	0.10 \pm 0.14
Total	Below 900	1.36 \pm 0.08	3.84 \pm 2.07	6.68 \pm 2.43
	Above 900	0.16 \pm 0.11	0.55 \pm 0.53	2.59 \pm 0.87

to elevated temperatures and droughts might contribute to the successful survival of these tree species in the region.

The presence of Scots pine and European larch is an essential prerequisite for resistance of stands to most abiotic harmful agents, especially windstorms, and risks posed by pests, mainly bark beetles, and fungal diseases (Lindner et al 2010; Blennow 2012; Konôpka, Zach, et al 2016; Kacálek et al 2017). Unanswered questions still remain regarding the future of currently rarely occurring tree species in the area, such as silver fir and European beech (*Fagus sylvatica* L.). These may spontaneously expand to this region, or they be planted here and theoretically prosper due to changing ecological conditions. Thus,

introduction of these tree species to the TANAP should be studied further.

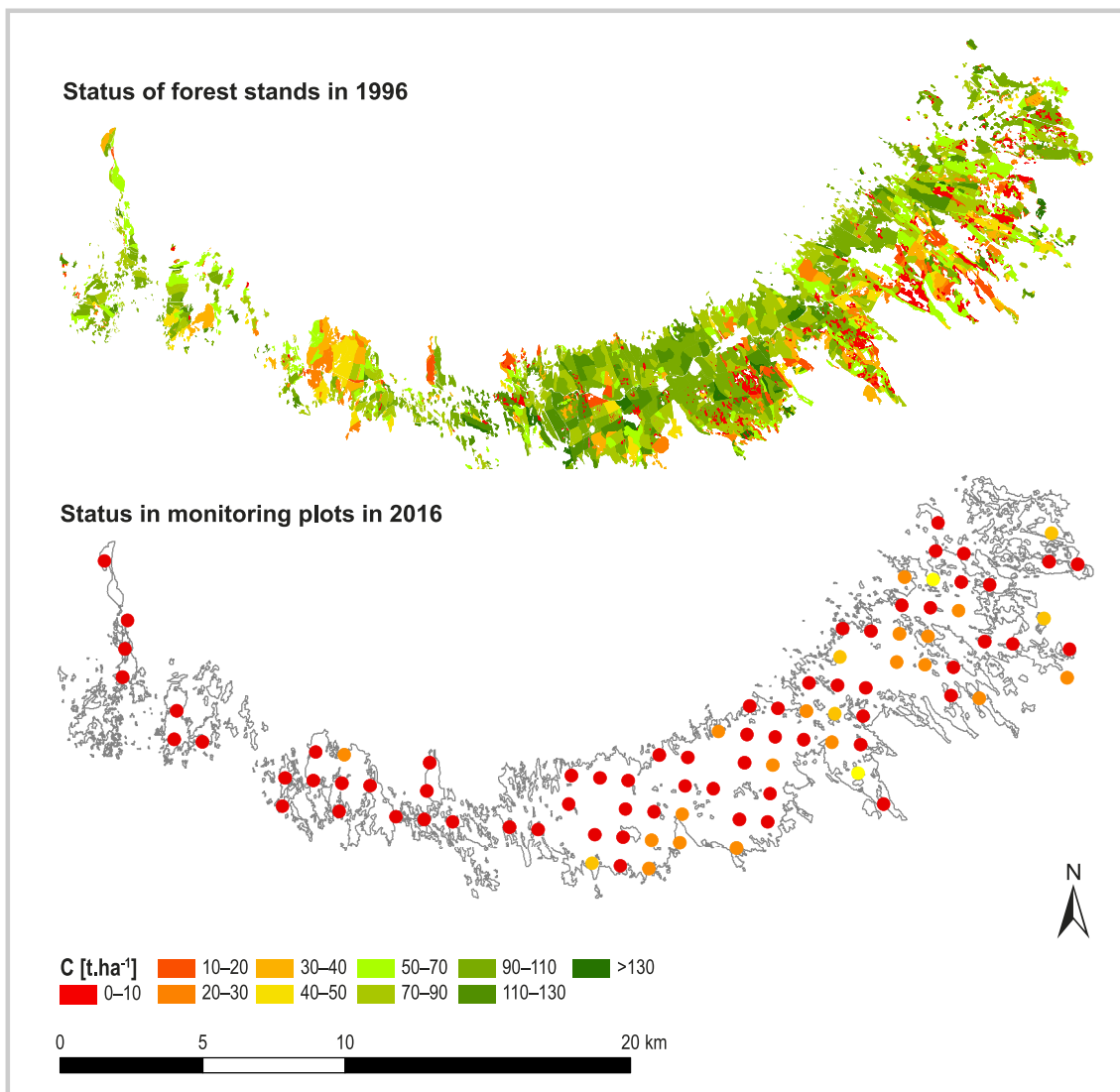
Carbon pool in whole-tree biomass

One of the most serious negative consequences of large-scale forest disturbances is the dramatic decline in carbon pool in tree biomass. Our estimates show that the average carbon pool in forest biomass was around 8 t per hectare in 2016, representing about 8% of the amount that existed before the windstorm (year 1996). In 2016, the carbon stock in whole-tree biomass at elevations below 900 m was approximately twice as high as that at elevations above 900 m. This finding is in accordance with work by Fleischer et al (2017), which showed fast recovery

TABLE 3 Carbon stock in the whole-tree biomass of the different broadleaved species according to years measured and elevational zones (mean values \pm double values of standard errors, ie 95% confidence intervals).

Broadleaved species	Elevational zone (m above sea level)	Carbon stock per year (t ha^{-1})		
		2007	2010	2016
Birches	Below 900	0.14 \pm 0.13	0.76 \pm 0.53	2.82 \pm 1.69
	Above 900	0.01 \pm 0.02	0.15 \pm 0.17	1.37 \pm 0.98
Rowan	Below 900	0.13 \pm 0.12	0.32 \pm 0.20	0.26 \pm 0.38
	Above 900	0.13 \pm 0.13	0.47 \pm 0.43	0.84 \pm 0.51
Goat willow	Below 900	0.06 \pm 0.07	0.17 \pm 0.10	0.29 \pm 0.22
	Above 900	0.05 \pm 0.11	0.14 \pm 0.11	0.46 \pm 0.27
Others	Below 900	0.24 \pm 0.37	0.58 \pm 0.61	1.44 \pm 0.94
	Above 900	0.01 \pm 0.01	0.02 \pm 0.04	0.05 \pm 0.04
Total	Below 900	0.58 \pm 0.34	1.83 \pm 1.19	4.80 \pm 1.87
	Above 900	0.20 \pm 0.13	0.77 \pm 0.39	2.72 \pm 1.28

FIGURE 5 Estimation of carbon pool in forest (whole-tree) biomass before the disturbance (top) and after the disturbance (bottom).



at mountain foothills and postponed recovery on high-elevation slopes. The differences arise from different growth conditions, especially climatic, soil, and topographic properties. Recovery and productivity of postdisturbance forest stands are likely caused by contrasting water regimes of soils in the foothill zone (high water saturation) and the mountain zone (low water content) (Anonymous 2012). At the same, the differences in tree biomass stocks between the two elevational zones may relate to different postdisturbance management regimes. For instance, Michalová et al (2017) showed that salvage logging in the TANAP influenced forest recovery by decreasing the density of spruce seedlings and increasing tree species diversity, at least at initial development stages.

The current levels of carbon accumulated in whole-tree biomass in the TANAP seems very unfavorable in

comparison with that before the disaster. On the other hand, it must be taken into account that the young forest stands are very dynamic (high biomass increase in few years), and so they are currently absorbing large amounts of carbon from the atmosphere annually (Konôpka et al 2017). Here, we would like to point out that much carbon is sequestered in ground vegetation and especially in the soil. However, these parts of the forest ecosystem were not part of our research. In general, intensive ground vegetation growth mitigates carbon loss after forest disturbance (Zehetgruber et al 2017). In the TANAP, dense ground vegetation appeared in 2006, 2 years after the windstorm, reaching maximum abundance in 2009 and 2010 (Fleischer et al 2015). As time passed after the disturbance, gradually decreasing ground vegetation biomass and increasing tree biomass appeared due to mutual competition. Our previous study (Konôpka et al

2017) found that on foothill sites of the TANAP postdisturbance area, trees represented approximately 80% and ground vegetation represented 20% of total aboveground vegetation biomass 12 years after the wind disturbance (ie in 2016). Regarding forest soils, Axel et al (2012) found no rapid carbon loss 1–5 years after the windstorm in the High Tatra Mountains. Hence, we can assume that the rapid colonization of ground vegetation and later tree growth played an important role in stabilizing the level of soil carbon in the TANAP territory.

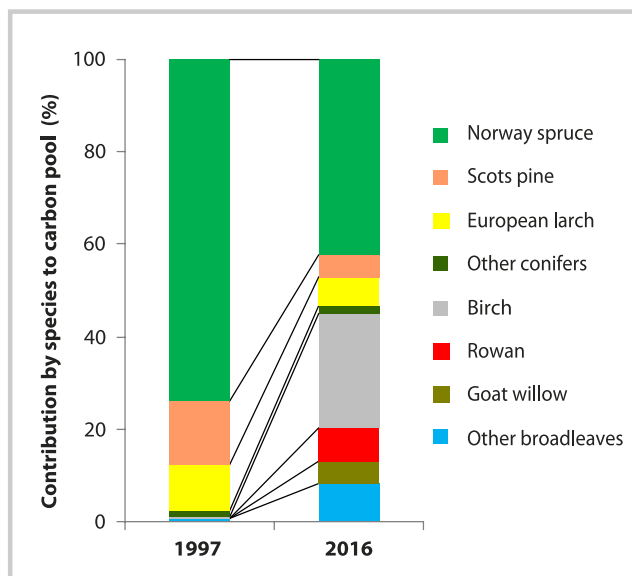
Nature conservation requirements affected the results presented here: Indeed, a considerable part of the wood was not processed but just left on the disturbance area. For instance, the monitoring of the revitalization processes (Šebeň 2011b) showed as much as $110 \text{ m}^3 \text{ ha}^{-1}$ of dead wood in the TANAP. This is almost $1,000,000 \text{ m}^3$ of wood for the whole disturbed area, with snags making up about 4%, stumps 22%, and lying trees 74% of the total (of which 45% was merchantable wood and 29% was composed of thin woody components, ie with a diameter under 7 cm).

Conclusions and recommendations

Our findings suggest a relatively positive tendency of forest development in the TANAP area after the 2004 windstorm, since a substantial part of its surface is now covered by young mixed forests. Nature itself contributed greatly though spontaneous regeneration, but foresters also contributed through artificial restoration. Reliable artificial regeneration has probably helped to increase species diversity, found mainly at lower elevations. The increased share of European larch and Scots pine should improve stability (ie wind resistance) of forest stands in future. On the other hand, some uncertainties exist regarding the sustainability of larch in the mountain zone of the TANAP due to changing climate conditions. A relatively high proportion of broadleaved species, especially rowan and goat willow, would mitigate potential damage to the long-living tree species caused by red deer (the population density of which is too high in the area) (Konôpka et al 2018).

As of 2016, by comparison with the predisturbance period (reference year 1996), the postdisturbance stands stored approximately one twelfth of the carbon in whole-tree biomass. However, it is worth mentioning that the dynamic development of young forest stands is

FIGURE 6 Contribution of tree species to carbon pool in the total whole-tree biomass in the windthrow area before the disturbance (in 1996) versus after the disturbance (measured in 2016).



remarkable, as they represent a large carbon amount absorbed annually from the atmosphere. In addition, in the postdisturbance area, a considerable amount of carbon is still fixed in the dead wood, such as snags, stumps, roots, and lying trees. Gradual decomposition of this carbon stock may last 20 or more years, with piecemeal carbon emission occurring continuously.

Continuous (ideally 30 year) monitoring of forest development based on a network of plots would be important. Observations should focus not only on basic forest inventory characteristics (eg species composition, stand density, and biomass stock), but also on tree health status and occurrence of pests. In the managed part of TANAP, foresters should aim to maintain as rich a species composition as possible. At the same time, silvicultural interventions should sustain a heterogeneous spatial structure, mainly with height differences among tree groups, creating complex forest sites at micro- and mesoscales. Forest management should not interfere with natural differences between forest regeneration rates in foothill and mountain areas. Finally, foresters must support these differences at the macroscale using differentiated management, especially with regard to the timing and intensity of silvicultural measures.

ACKNOWLEDGMENTS

The research was supported by project APVV-14-0086 from the Slovak Research and Development Agency as well as by grant EVA4.0, no. CZ.02.1.01/0.0/0.0/16_019/0000803, financed by Operational Program Research and Development.

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