



Aboveground Net Primary Production of tree cover at the post-disturbance area in the Tatra National Park, Slovakia

Čistá primárna produkcia nadzemnej časti stromovej vegetácie na postdisturbančnom území Tatranského národného parku, Slovensko

Bohdan Konôpka^{1,2*}, Jozef Pajtík^{1,2}, Vladimír Šebeň¹, Michal Bošela^{1,2}

¹National Forest Centre - Forest Research Institute Zvolen, T. G. Masaryka 2175/22, SK – 960 92 Zvolen, Slovakia

²Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129, CZ – 165 21 Praha 6 - Suchbátka, Czech Republic

Abstract

Large-scale disturbances under the conditions of Slovakia, caused especially by storm and bark beetle, bring dramatic decline in carbon budget of the country, besides other negative consequences. The largest disturbance in modern history of the Slovak forestry was the storm damage that occurred in November 2004. The Tatra National Park (TNP) was one of the most affected regions. Thus, in this territory, two transects (T1 – the Danielov dom site and T2 – near the Horný Smokovec village) were established to survey basic dendrometric properties of trees in young stands established after the disaster. The standing stock of aboveground biomass in tree cover for the spring and autumn 2014 was calculated using the recorded variables, i.e. tree height and diameter measured at the stem base, together with the region-specific allometric relations. Then, the Aboveground Net Primary Production (ANPP) in tree cover was estimated with respect to its components (stem, branches and foliage). ANPP was 315 g m⁻² per year (Transect T1), and 391 g m⁻² per year (Transect T2). The differences in the structure of ANPP, i.e. contribution of tree components, were found between transects T1 and T2. They were caused by the contrasting tree species composition, specifically the ratios between Norway spruce and broadleaved species. Broadleaves allocated more biomass production to foliage than spruce. This phenomenon together with higher turnover (once a year) of foliage caused that broadleaves manifest higher share of fast-cycling carbon in comparison to the amount of carbon sequestered in woody parts (stem and branches). High variability of ANPP was found within the transects, i.e. among the plots (microsites). As for the representative estimation of the standing stock of aboveground part of tree cover as well as ANPP at the post-disturbance area in the TNP territory, the survey should be performed on a net of research plots. Only this approach enables reliable estimates of carbon amount sequestered in woody parts, eventually carbon yearly absorbed by young forest stands.

Keywords: aboveground standing stock; broadleaved trees; Norway spruce; tree components; young forest stands

Abstrakt

Veľkoplošné disturbance, v podmienkach Slovenska hlavne vetrové a podkôrníkové, spôsobujú okrem iných negatívnych následkov dramatické zhoršenie uhlíkovej bilancie v krajine. Najrozsiahlejšou disturbanceou v novodobej histórii slovenského lesníctva bola vetrová kalamita v novembri 2004. Pritom Tatranský Národný Park (TANAP) bol jedným z najviac postihnutých území. V tomto regióne sme na dvoch vybraných tranzektoch (T1 – lokalita Danielov dom a T2 – pri Hornom Smokovci) sledovali základné dendrometrické znaky drevín v mladých porastoch vzniknutých na kalamitných plochách. Prostredníctvom zistených hodnôt, t. j. výšky stromov a hrúbky kmeňa meranej na úrovni pôdy (nezávislé premenné) a alometrických vzťahov sa vypočítala zásoba nadzemnej biomasy na jar a jeseň 2014. Následne sa odhadla čistá primárna produkcia nadzemnej časti (ANPP) stromovej vegetácie podľa komponentov (kmeň, konáre a asimilačné orgány). ANPP bola 315 g.m⁻² za rok (tranzekt T1), resp. 391 g.m⁻² za rok (tranzekt T2). Medzi tranzekdami boli rozdiely v štruktúre ANPP vzhľadom na podiel stromových komponentov. Dôvodom bolo rôzne drevinové zloženie, konkrétne pomer medzi smrekom a listnácami. Listnáče oproti smreku alokovali vyšší podiel biomasy do asimilačných orgánov. Tento jav spolu s jednoročným cyklom obehu asimilačných orgánov spôsobujú, že pri listnáčoch je vyšší podiel „rotujúceho“ uhlíka ku kvantite uhlíka dlhodobovo viazaného v drevených častiach (kmeň a konáre). Veľká variabilita ANPP sa zistila v rámci každého tranzektu, t. j. medzi plochami (mikrostanovišťami). Pre reprezentatívny odhad zásoby stromovej biomasy a ANPP na postdisturbančnom území TANAP-u treba takéto merania zabezpečiť na sieti výskumných plôch. Až takýto postup umožní spoľahlivý odhad množstva uhlíka viazaného v drevenej biomase, resp. objemu uhlíka každoročne absorbovaného lesnou vegetáciou.

Kľúčové slová: zásoba nadzemnej biomasy; listnaté dreviny; smrek obyčajný; stromové komponenty; mladé lesné porasty

1. Introduction

Although so far no direct scientific evidence exists for more frequent occurrence and higher velocity of winds as a consequence of climate change, a review book by Gardiner et al. (2011) has shown a gradually increasing number of dis-

turbance episodes caused by windstorms in the European forests. Destruction of forest stands, especially in the case of delayed forest cover regeneration brings deterioration in carbon budget at a regional scale (Dale et al. 2001). The carbon losses are mainly due to the decreased amount of above-

*Corresponding author. Bohdan Konôpka, e-mail: bkonopka@nlcsk.org, phone. +420 5314 323

ground biomass (Kurz & Apps 1999) and stimulated carbon emission from the soil environment (Lal & Follett 2009). Hence, mutual stimulation may arise between the phenomena: climate change → disturbance of forest ecosystems → climate change.

Liu et al. (2011) showed a sharp decrease in soil carbon content, litter and especially in biomass (considering all parts of forest ecosystem, however, dominated by trees) after disturbances of forest cover. Reaching the original status (pre-disturbance) usually takes a couple of decades and carbon losses relate to timing of forest regeneration. To evaluate the absorption of carbon from the air by vegetation it is necessary to define the Net Primary Production (NPP). The NPP represents the energy (eventually the amount of produced biomass or carbon absorbed in the form of CO₂) accumulated in plants via a process of photosynthesis after subtracting a part of energy consumed for respiration (e.g. Waring et al. 1998). In fact, the NPP at a tree or stand level equals biomass (if appropriate carbon) of all tree components created in certain period, usually expressed for one year. The quantification of NPP in the specific types of forest ecosystems, or their different growth stages has not been performed in the conditions of Slovakia yet. Only few partial works exist (e.g. Konôpka et al. 2013; Pajčík et al. 2013). Moreover, there is a lack of results dealing with NPP estimated for a variety of forest communities in different ecological conditions also in other developed countries. Actually most of the existing studies related to NPP omitted some tree components, most frequently belowground biomass (e.g. Zianis et al. 2005; Kho et al. 2013).

For estimations of biomass stock and production, and eventually their structure, it is necessary to have mathematical models parameterised for a specific region. During the last two to three decades the models for the quantification of biomass in tree components of the most important forest tree species were constructed by many European scientific groups, usually by means of allometric relations or expansion factors (Chroust 1985; Chroust & Tesařová 1985; Marklund 1987; Cienciala et al. 2006; Tobin & Nieuwenhuis 2007; Seidl et al. 2010; Skovsgaard et al. 2011; Pajčík et al. 2011a and some others). Wirth et al. (2004) pointed out that almost all works focused on the construction of models for trees with stem diameter (dbh; measured at 130 cm height from the ground level) over 7 cm. Therefore, the biomass models for young (small) trees are missing. Thus, for instance, in the case of Norway spruce (*Picea abies*), allometric equations were constructed exclusively for young stands from natural regeneration in Slovakia (Pajčík et al. 2008) and for young stands planted on former pastures in Romania (Dutca et al. 2010).

In modern history of Slovak forestry, the largest disturbance episode happened on 19th November 2004. The windstorm damaged the forest stands on leeward sites, i.e. on southern and south-eastern slopes in the Low Tatra and especially High Tatra mountains. Besides the Tatra Mountains, some wind disturbances occurred in the Orava region and the Slovak Ore Mountains. The wind disturbance affected 12 thousand hectares of forests within the territory of the Tatra National Park (hereinafter TNP; Koreň 2005). Consequently, bark beetle outbreak spread over a large area and devastated neighbouring spruce stands (Nikolov et al. 2014).

In addition, another windstorm accompanied by intensive rainfall (on May 14th and 15th, 2014) damaged the remaining forest stands at the territory of the TANAP (Gubka et al. 2014). Thus, two wind disasters and bark beetle outbreak caused the reduction of old-forest area to 1/10 of the former acreage (considering the situation before 2014). It means that 90% of the former forest area is either nearly treeless or covered by young forest stands aged up to 10 years.

The previous surveys conducted at the TNP area (Kaštier & Bučko 2010; Šebeň 2011a, 2011b) indicated that the young post-disturbance stands are composed prevalently by: Norway spruce, rowan (*Sorbus aucuparia*), birches (prevalently *Betula pendula*), goat willow (*Salix caprea*), and at some sites also larch (*Larix decidua*), and Scots pine (*Pinus sylvestris*). Therefore, for the calculation of the standing stock of these forest stands local allometric models, especially for these species, are necessary. In the previous activities, we constructed such models for Norway spruce (Pajčík et al. 2008) and Scots pine (Pajčík et al. 2011a) at a national level. Moreover, we collected tree samples also in the area of the TNP and constructed region-specific allometric functions for rowan (Pajčík et al. 2015a), goat willow (Pajčík & Konôpka 2015) and larch (Pajčík et al. 2015b).

The aim of the paper is to estimate the standing stock of the aboveground biomass in tree cover at the selected sites of post-disturbance area in the TNP in the spring 2014 and autumn 2014. The paper further focuses on estimating the Aboveground Net Primary Production (hereinafter ANPP) in the tree cover ten years after the large-scale wind damage as well as its structure by components (stem, branches and foliage).

2. Material and Methods

2.1. Site description

The research activities were conducted at a post-disturbance area after the intensive windstorm that happened in the TNP on 19th November 2004. The storm damaged mostly forests at altitudes between 700 and 1,400 m a.s.l. in the TNP concentrated prevalently in a continual belt oriented in a west-east direction, approximately 35 km long and 5 km wide (Šebeň 2011a). The forest soils at the post-disturbance area consist mainly of cambisols and podzols. The bedrock is predominantly formed of granodiorite. The climate is characterised by low mean annual temperatures (cca 4.0 °C), high precipitation totals (about 1,000 mm) and nearly 140 days of snow cover (Vološčuk et al. 1994).

In 2014 (the tenth growing season after the disturbance incident), the area was prevalently covered by young forests that originated from both natural regeneration and planting. Open areas between the young forest stands were covered by grasses (e.g. *Calamagrostis* sp., *Avenella flexuosa*, *Luzula luzuloides*), herbs (e.g. *Epilobium angustifolium*, *Senecio nemorensis*, *Rubus idaeus*) and shrubs (mostly *Vaccinium myrtillus*, *Sambucus racemosa*). At the beginning of the growing season 2014, we established two research transects – one near the site called “Danielov dom” (hereinafter T1) and another close to the Smokovce village (hereinafter T2;

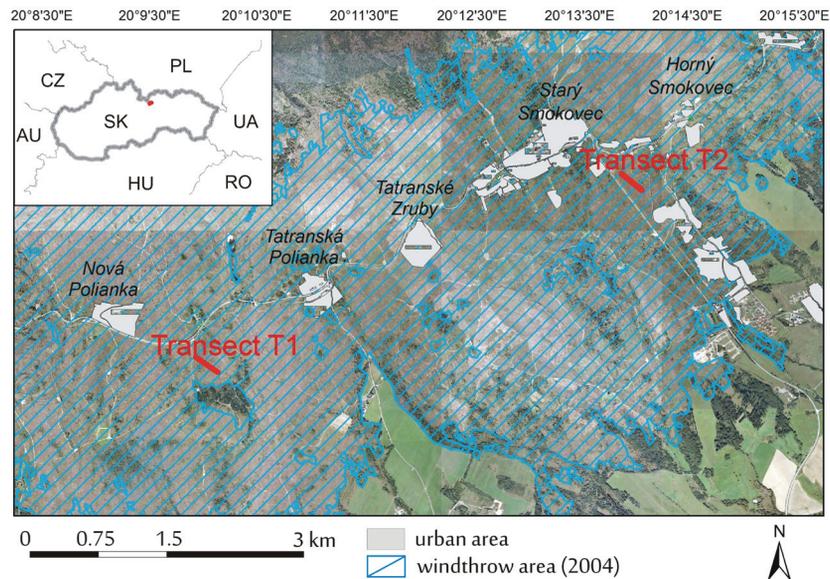


Fig. 1. Localisation of transect T1 (Danielov dom) and transect T2 (Horný Smokovec) at the Tatra National Park.

see also Figure 1). The sites belong to the territories of Tatranské Matliare and Horný Smokovec which are Protective Units managed by the State Forests of the TNP. The transects were established in the central part of the disturbed belt and they differed in the species composition of the forest stands. Specifically, T1 transect represented the stands dominated by Norway spruce, and T2 transect was covered with the stand dominated by broadleaved species. The orientation of both transects is from Northwest to Southeast, altitude of T1 is between 945 and 995 m a.s.l, and of T2 is from 925 to 970 m a.s.l.

2.2. Field work and calculations

The transects were 4-m-wide including 4-m-long plots with measured trees isolated by 8-m-long gaps without any measurements to ensure that the measured plots were not mutually influenced. Thus, every square plot (area 4×4 m) represented an independent entity for the estimation of standing stock and ANPP of tree cover. In total, each transect was approximately 300 m long and included 25 plots. Height and stem diameter at ground level (d_0 hereinafter) of all young trees including annual seedlings inside the plots were measured. At T1, around 400 individuals were subjected to the measurements at the beginning and the end of the growing season 2014. At T2, the number of measured trees was nearly 600.

The data on tree height and diameter d_0 were used in species-specific allometric models for the calculation of aboveground biomass at a tree level. The allometric models originated mostly from our previous papers (Konôpka et al. 2010; Konôpka et al. 2015; Pajčík & Konôpka 2015; Pajčík et al. 2015a,b). The allometric models express particular aboveground tree components, i.e. stem (Appendix 1a), branches (Appendix 1b) and foliage (Appendix 1c). Biomass estimates were calculated for each tree at the plots. Afterwards, standing stock of aboveground biomass in tree vegetation was calculated for each plot. Finally, mean standing biomass (grams

per m^2) was expressed for two periods, i.e. the beginning and the end of the growing season 2014, and for each transect.

The NPP of aboveground components was estimated as a combination of plot-specific and species-specific measurements. Thus, NPP at each plot was calculated as a sum of productions of individual tree species growing on the plot. NPP of branches and stems was expressed as a difference between their standing stock in autumn (before fall of foliage) and spring (before bud burst). The same procedure was used for NPP of foliage in broadleaved species and larch. In the case of spruce, NPP of needles was calculated as 1/6 of their autumn standing stock (it relates to number of age-classes; see e.g. Schmidt-Vogt 1977) and for pine as 1/3 of needle standing stock in autumn (e.g. Konôpka 2003). The mean NPP was calculated separately for each transect by averaging NPP from all the plots of the specific transect. Mean NPP (gram per m^2 per one growing season or per year) for each transect was estimated by the tree components.

Data manipulation was performed in Excel, and calculations and analyses were performed in Statistica 10.0 and FoxPro. The Student's t-test (considering $\alpha = 0.05$) was used to determine the significance of the differences in the standing stock of aboveground biomass and ANPP in tree cover between transects T1 and T2 or between the spring and autumn.

3. Results and discussion

The results indicated high spatial variability (i.e. differences between plots) in tree density and basic tree characteristics (Table 1). As for the differences between transects T1 and T2, similar values of mean diameter d_0 and tree height were found. On the other hand, tree density and standing stock (expressed on area measured at the ground level) were higher at transect T2. Great differences between transects T1 and T2 were found in tree species composition (Table 2). While the stands at transect T1 were spruce dominated

(contribution of 78% to total number of trees), transect T2 was prevalingly dominated by broadleaved species such as rowan, goat willow and birch. Although spruce was the most frequent species, it represented only around 41% of the total number of trees. Considering the situation at both transects, we identified nine tree species (Table 2), out of which six were broadleaved (grey alder, sycamore maple, silver birch, rowan, goat willow, trembling aspen) and three coniferous (spruce, Scots pine and larch).

We analysed tree height frequency distribution in the spring and autumn 2014 for spruce and rowan (Fig. 2a and 2b). While most of the spruce trees were at a height class 51 – 100 cm, most rowans were at a height class of 101 – 150 cm. Another difference between the species was found for the height class over 400 cm, in which much more rowans occurred than spruces. These differences indicated faster height growth of rowan than spruce even though terminal browsing by red deer was observed for rowan with higher frequency (data not shown). Similar finding was obtained by Šebeň et al. (2015) for natural generation recorded in the declining spruce stand in the TNP. Interesting results were also found for the height class up to 50 cm. While the

number of rowan trees increased during the growing season, the opposite tendency was found for spruce. It seems that the natural regeneration of rowan (individuals established in 2014) was more intensive than that of spruce.

The estimates of standing stock of aboveground biomass in tree cover indicated only a small (insignificant; Student’s t-test considering $p = 0.05$) difference between transects T1 and T2 (Table 3). While in the spring the standing stock was 636 g m^{-2} and 788 g m^{-2} at transects T1 and T2, respectively, in the autumn the standing stock at T1 was 950 g m^{-2} and 1054 g m^{-2} at T2. The standing stock of the aboveground part in tree cover increased during the growing season by 49% and 34% at transects T1 and T2, respectively. If we consider a hectare base (a generally recognised unit in forestry practice), the standing stock of the aboveground biomass in tree cover at transect T1 was 6.4 t of dry matter (i.e. cca 3.2 t of carbon) in the spring and 7.9 t of dry matter (cca 4.0 t of carbon) in the autumn. Similarly at transect T2, the standing stock was 9.5 t of dry matter (i.e. cca 4.8 t of carbon) per ha in the spring and 10.5 t of dry matter (cca 5.3 t of carbon) per ha in the autumn.

Table 1. Basic stand characteristics for the plots at transect T1 (Danielov dom) and at transect T2 (Horný Smokovec). Mean values and standard deviations (in brackets) are shown. The differences between transects T1 and T2 were not significant (Student’s t-test, $\alpha = 0.05$).

Transect	Season of 2014	Number of trees per plot	Number of tree species per plot	Diameter d_0 [mm]	Height h_{Lorey}^* [m]	Basal area G_0 [$\text{cm}^2 \cdot \text{m}^{-2}$]
T1	Spring	15 (± 24)	2 (± 1)	35.2 (± 18.8)	2.25 (± 1.14)	6.67 (± 5.66)
	Autumn	15 (± 25)	2 (± 1)	40.2 (± 21.7)	2.66 (± 1.33)	9.59 (± 7.13)
T2	Spring	24 (± 25)	4 (± 1)	35.3 (± 18.2)	2.92 (± 1.36)	10.52 (± 5.81)
	Autumn	23 (± 25)	4 (± 1)	38.3 (± 21.7)	3.29 (± 1.32)	14.11 (± 9.22)

Explanatory note: * h_{Lorey} – Lorey’s mean height.

Table 2. Contribution of tree species (in percent, calculated from the total number of trees) at transect T1 (Danielov dom) and transect T2 (Horný Smokovec).

Transect	Season of 2014	<i>Acer pseudoplatanus</i>	<i>Alnus incana</i>	<i>Betula pendula</i>	<i>Larix decidua</i>	<i>Picea abies</i>	<i>Pinus sylvestris</i>	<i>Populus tremula</i>	<i>Salix caprea</i>	<i>Sorbus aucuparia</i>
T1	Spring	0.3	0.0	2.7	4.6	77.6	0.3	1.3	6.2	7.0
	Autumn	0.5	0.0	2.7	4.3	78.2	0.5	3.2	5.8	4.8
T2	Spring	1.8	1.2	13.5	1.3	41.7	1.8	0.8	19.3	18.6
	Autumn	1.4	1.1	13.5	1.1	41.4	1.4	1.2	16.7	22.4

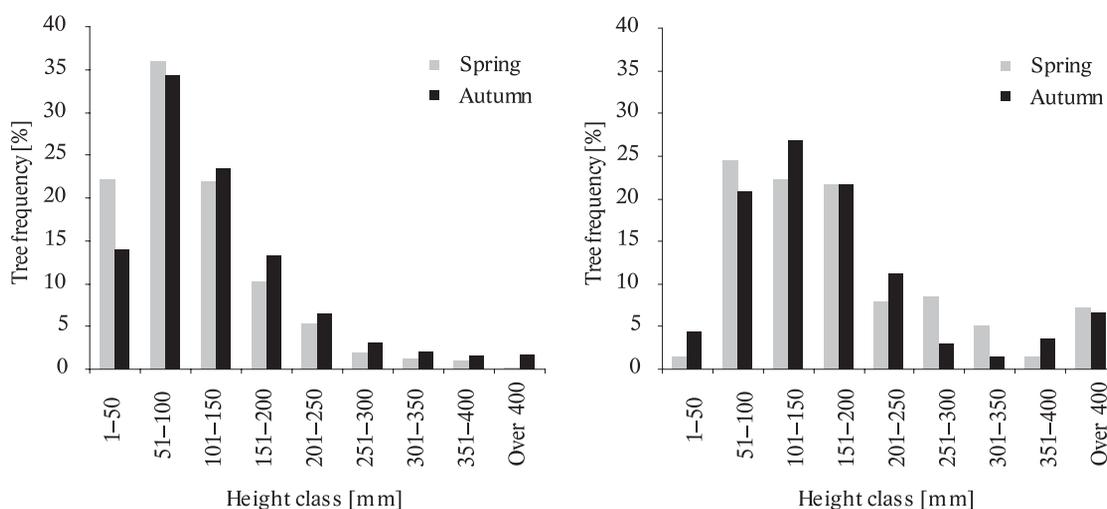


Fig. 2. Tree frequency of Norway spruce (left) and rowan (right) by height classes at transect T1 (Danielov dom) and transect T2 (Horný Smokovec) in the spring 2014 and autumn 2014.

Table 3. Standing stock of aboveground biomass in tree cover by components at transect T1 (Danielov dom) and transect T2 (Horný Smokovec). Mean values and standard deviations (in brackets) are shown. The differences between transects T1 and T2 or between the spring and autumn were not significant (Student's t-test, $\alpha = 0.05$).

Transect	Season of 2014	Stem	Branches	Foliage	Aboveground parts of trees
		[g m ⁻²]			
T1	spring	261 (±276)	234 (±285)	141 (±174)	636 (±735)
	autumn	365 (±354)	333 (±350)	252 (±220)	950 (±924)
T2	spring	428 (±285)	297 (±285)	63 (±137)	788 (±707)
	autumn	501 (±371)	344 (±367)	209 (±208)	1054 (±924)

Certain differences were found in the proportion of standing stock components not only between the spring and autumn but also between transects T1 and T2 (Fig. 3). The differences between the spring and autumn standing stock related mainly to different foliage quantities in deciduous species (broadleaved trees and larch). Thus, the composition of the standing stock changed from spring to autumn more at transect T2 (prevalingly broadleaved trees) than at T1 (dominance of spruce). At transect T1, stem contributed to standing stock most (41% and 38% in the spring and autumn, respectively), and foliage least (22% and 27% in the spring and autumn, respectively). At transect T1, the highest contribution to standing stock was found for stem (54% and 48% in spring and autumn, respectively) and lowest for foliage (8% and 20% in spring and autumn, respectively).

ANPP of tree cover was slightly, but not significantly (Student's t-test considering $p = 0.05$) greater at transect T1 (315 g m⁻² per year) than at T2 (391 g m⁻² per year; Table 4). On the other hand, large variability among the plots was revealed (Fig. 4). For instance at transect T1, ANPP varied from 0 (tree-less plots 13 and 24) to nearly 1,200 g m⁻² per year. We could not find any clear pattern in spatial variability along the transects – plot number 1 was situated at the highest (995 m a.s.l. at T1 and 945 m a.s.l. at T2) and plot number 25 at the lowest altitude (970 m a.s.l. at T1 and 925 m a.s.l. at T2). The differences in ANPP of tree cover between the plots were most probably related to the actual state of the old (reproductive) tree cover and micro-site con-

ditions. Certain differences between the transects were found also in the composition of ANPP by components (Fig. 5). While a rather balanced contribution of components was found at T1 (stem – 33%, branches – 32%, foliage – 35%), contrasts between the components (stem – 26%, branches – 34%, foliage – 40%) occurred at T2.

Our results indicated that young stands with the dominance of spruce invested less proportion of carbohydrates to foliage (fast carbon cycling component) than the stands with the prevalence of broadleaved species. Moreover, forasmuch as broadleaved trees species rotate their whole foliage every year and spruce only one sixth of its foliage, we can assume much higher quantity of carbon cycled in broadleaves than in spruce. Our results on ANPP of tree cover and its structure could not be confronted with the findings from other works.

Table 4. ANPP in tree cover by components at transect T1 (Danielov dom) and transect T2 (Horný Smokovec). Mean values and standard deviations (in brackets) are shown. The differences between transects T1 and T2 were not significant (Student's t-test, $\alpha = 0.05$).

Transect	Stem	Branches	Foliage	Aboveground parts of trees
	[g.m ⁻²]			[g m ⁻² per year]
T1	105 (±110)	99 (±97)	111 (±83)	315 (±290)
T2	101 (±120)	134 (±287)	156 (±92)	391 (±499)

The main reason is that the previous research focused exclusively on older forest stands (e.g. Xiao et al. 2003; Tateno et al. 2004; Yuste et al. 2005; Zianis & Mencuccini 2005). Only our previous study (Pajtk et al. 2013) in young spruce and beech (*Fagus sylvatica*) stands showed that while the contribution of foliage to standing stock of aboveground biomass was much larger in spruce than in beech, the share of foliage to ANPP was nearly at the same level in both species. Very probably, the structure of ANPP does not vary only between different species but might change with the age of trees. For instance, Pajtk et al. (2011b) showed that in the biomass allocation of young beech and oak (*Quercus petraea*) stands the contribution of foliage was rather stable, but clear changes occurred in the ratio between stem and branch quantity.

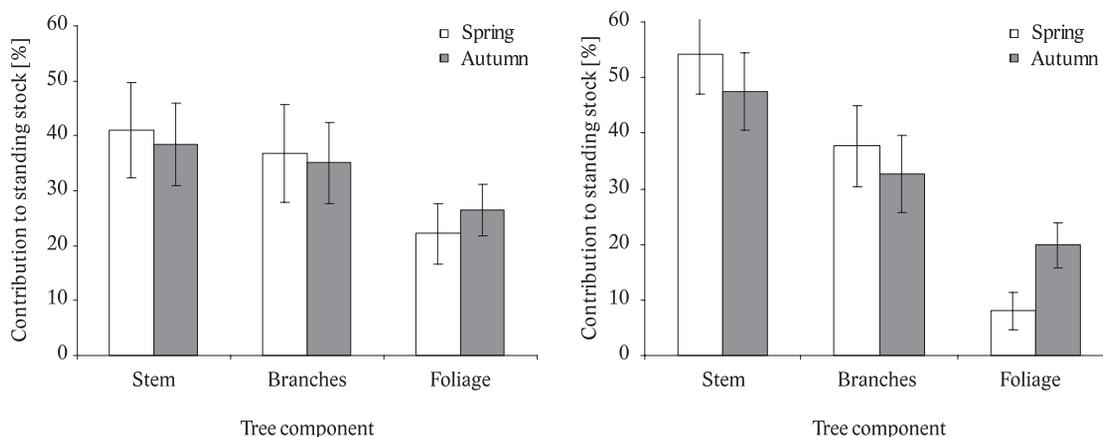


Fig. 3. Contribution of tree components to standing stock in the spring 2014 and autumn 2014 at transect T1 (Danielov dom; left) and transect T2 (Horný Smokovec; right). Mean values and standard errors are shown. The differences between the transects were significant (Student's t-test, $\alpha = 0.05$) only for the contribution of foliage in the spring, and for the seasonal (spring versus autumn) contribution of foliage at transect T2.

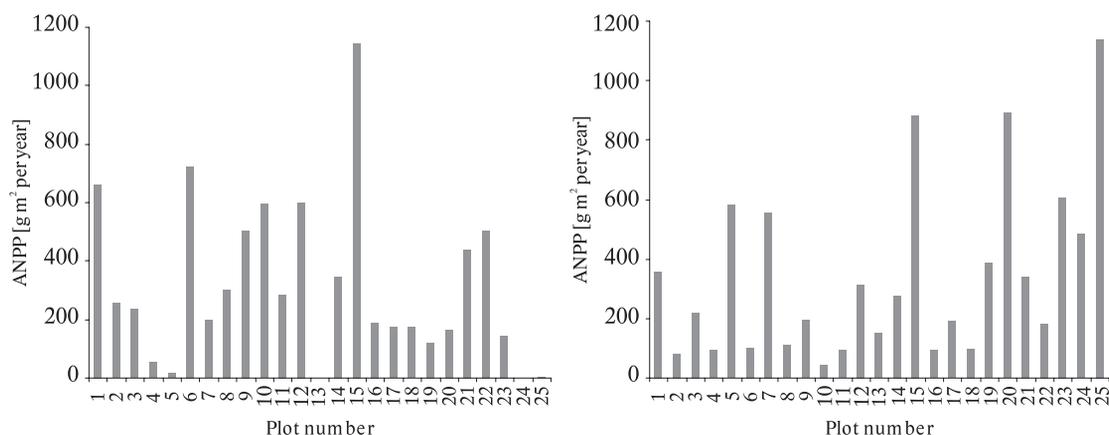


Fig. 4. ANPP of tree cover in 2014 at transect T1 (Danielov dom; left) and transect T2 (Horný Smokovec; right) by each plot.

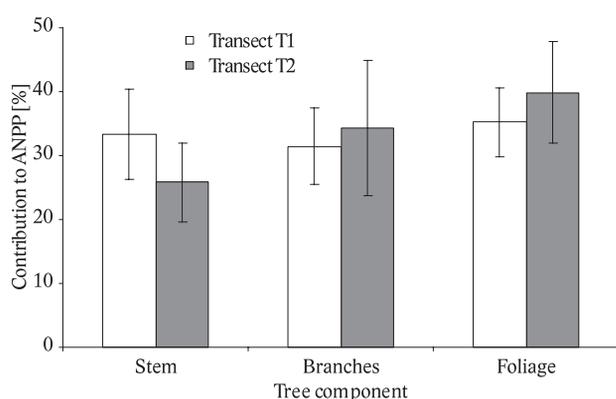


Fig. 5. Contribution of tree components to ANPP in 2014 at transect T1 (Danielov dom) and transect T2 (Horný Smokovec). Mean values and standard errors are shown. The differences between the transects were not significant (Student's t-test, $\alpha = 0.05$).

4. Conclusions

The results indicated that although the standing stock of the aboveground biomass in young post-disturbance tree cover was rather small (between 6.3 and 10.5 t.ha⁻¹), its annual production was relatively large (3.2 and 3.9 t.ha⁻¹ per year at transects T1 and T2, respectively). We did not find clear differences in the standing stock and ANPP between the transects (even though they had different tree species compositions). Certain contrast between transects T1 and T2 was found in the structure (regarding tree components) of standing stock and ANPP. These differences were probably caused by the variability in the proportion of spruce and broadleaved tree species. We found very large spatial variability in ANPP of tree cover that was perhaps related to the distribution of reproductive tree cover and micro-site (soil) conditions.

Seeing that our study in the TNP covered exclusively the aboveground parts of tree biomass, we plan to extend our future research also to belowground biomass standing stock and production as well as the total biomass of other plants (bushes, herbs and grasses). Moreover, biomass standing stock and production will be assessed on a net of plots representative for the area affected by the windstorm. Such a complex study will allow more reliable estimates of carbon

storage and rotation in vegetation cover accrued after the large-scale forest disturbance in the TNP.

Acknowledgements

The research was supported by the projects APVV-0273-11, APVV-0111-10, and APVV-14-0086 from the Slovak Research and Development Agency in the Slovak Republic. With additional thanks to project No. QJ 1220316 supported by the Ministry of Agriculture of the Czech Republic. Mr. Peter Fleischer and Peter Michelčík are acknowledged for their help with selection of the plots and fieldwork.

References

- Cienciala, E., Černý, M., Tatarinov, F., Apltauer, J., Exnerová, Z., 2006: Biomass functions applicable to Scots pine. *Trees*, 20:483–495.
- Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D. et al., 2001: Climate change and forest disturbances. *BioSciences*, 51:723–734.
- Dutca, I., Abrudan, I. V., Stancioiu, P. T., Blujdea, V., 2010: Biomass conversion and expansion factors for young Norway spruce (*Picea abies* [L.] Karst.) trees planted on non-forest lands in Eastern Carpathians. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, 38:286–292.
- Gardiner, B., Schuck, A. S., Schelgaas, M. J., Orazio, Ch., Blennow, K., Nicoll, B. et al., 2011: Living with storm damage to forests. European Forest Institute, Joensuu, 129 p.
- Gubka, A. et al. 2014: Vetrová kalamita Žofia z 15. 5. 2014. Usmernenie Lesníckej ochrannárskej služby, NLC, Zvolen, 8 p.
- Chroust, L., 1985: Above-ground biomass of young pine forests (*Pinus sylvestris*) and its determination. *Communications Instituti Forestalis Českosloveniae*, 14:127–145.
- Chroust, L., Tesařová, 1985: Quantification of above-ground components of 20 years old Norway spruce (*Picea abies* [L.] Karst.). *Communications Instituti Forestalis Českosloveniae*, 14:111–126.
- Kho, L. K., Malhi, Y., Tan, S. K. S., 2013: Annual budget and seasonal variation of aboveground and belowground net primary productivity in a lowland dipterocarp forest in Borneo. *Biogeosciences*, 118:1282–1296.
- Kaštier, P., Bučko, J., 2010: Analýza intenzity a dislokácie škôd spôsobených raticovou zverou na iniciálnych štádiách lesa po kalamite roku 2004 vo Vysokých Tatrách. In: Výskum smrečín destabilizovaných škodlivými činiteľmi. NLC Zvolen, p. 198–205.

- Konôpka, B., 2003: Needle traces as indicators of growing conditions in Scots pine (*Pinus sylvestris* L.). *Journal of Forest Science*, 49:1–10.
- Konôpka, B., Pajtík, J., Moravčík, M., Lukac, M., 2010: Biomass partitioning and growth efficiency in four naturally regenerated forest tree species. *Basic and Applied Ecology*, 11:234–243.
- Konôpka, B., Pajtík, J., Noguchi, K., Lukac, M., 2013: Replacing Norway spruce with European beech: A comparison of biomass and net primary production patterns in young stands. *Forest Ecology and Management*, 302:185–192.
- Konôpka, B., Pajtík, J., 2014: Similar foliage area but contrasting foliage biomass between young beech and spruce stands. *Lesnícky časopis - Forestry Journal*, 60:205–213.
- Konôpka, B., Pajtík, J., Šebeň, V., 2015: Biomass functions and expansion factors for young trees of European ash and Sycamore maple in the Inner Western Carpathians. *Austrian Journal of Forest Science*, 132:1–60.
- Koreň, M., 2005: Čo sa stalo 19. novembra 2004 v tatranskej oblasti? *Tatry*, 44:4–6.
- Kurz, W. A., Apps, M. J., 1999: A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecological Applications*, 9:526–547.
- Lal, R., Follett, R. F., 2009: Soil carbon sequestration and greenhouse effects. *Soil Science Society of America*, Madison, 366 p.
- Liu, S., Bond-Lamberty, B., Hicke, J. A., Vargas, R., Zhao, S., Chen, J. et al., 2011: Simulating the impacts of disturbances on forest carbon cycling in North America: Processes, data, models, and challenges. *Journal of Geographical Research*, 16:1–22.
- Marklund, L. G., 1987: Biomass functions for Norway spruce (*Picea abies* L. Karst.) in Sweden. *Umeå, Swedish University of Agricultural Sciences*, 27 p.
- Nikolov, Ch., Konôpka, B., Kajba, M., Galko, J., Kunca, A., Janský, L., 2014: Post-disaster management and bark beetle outbreak in Tatra National Park, Slovakia. *Mountain Research and Development*, 34: 326–335.
- Pajtík, J., Konôpka, B., Lukac, M., 2008: Biomass functions and expansion factors in young Norway spruce (*Picea abies* [L.] Karst) trees. *Forest Ecology and Management*, 256:1096–1103.
- Pajtík, J., Konôpka, B., Lukac, M., 2011a: Individual biomass factors for beech, oak and pine in Slovakia: a comparative study in young naturally regenerated stands. *Trees*, 25:277–288.
- Pajtík, J., Konôpka, B., Priwitzer, T., 2011b: Alokácia dendromasy v mladých porastoch buka obyčajného a duba zimného. *Zprávy lesníckeho výzkumu*, 56:291–300.
- Pajtík, J., Konôpka, B., Marušák, R., 2013: Above-ground net primary productivity in young stands of beech and spruce. *Lesnícky časopis - Forestry Journal*, 59:154–162.
- Pajtík, J., Konôpka, B., 2015: Quantifying edible biomass on young *Salix caprea* and *Sorbus aucuparia* trees for *Cervus elaphus*: estimates by regression models. *Austrian Journal of Forest Science*, 132:61–80.
- Pajtík, J., Konôpka, B., Bošela, M., Šebeň, V., Kaštier, P., 2015a: Modelling forage potential for red deer: A case study in post-disturbance young stands of rowan. *Annals of Forest Research*, 58:91–107.
- Pajtík, J., Konôpka, B., Šebeň, V., Michelčík, P., Fleischer, P., 2015b: Alokácia biomasy smrekovca opadávého prvého vekového stupňa vo Vysokých Tatrách. *Štúdie TANAP-u*, 11:229–241.
- Schmidt-Vogt, H., 1977: Die Fichte. Band I. Taxonomie - Verbreitung - Morphologie Ökologie - Waldgesellschaften. Hamburg and Berlin, Verlag Paul Parey 472 p.
- Seidl, R., Rammer, W., Bellos, P., Hochbichler, E., Lexer, M. J., 2010: Testing generalized allometries in allocation modeling within an individual-based stimulation framework. *Trees*, 24:139–150.
- Skovsgaard, J. P., Bald, C., Nord-Larsen, T., 2011: Functions for biomass and basic density of stem, crown and root system of Norway spruce (*Picea abies* [L.] Karst.) in Denmark. *Scandinavian Journal of Forest Research*, 26:3–20.
- Šebeň, V., 2011a: Prírodná obnova po kalamite z novembra 2004 vo Vysokých Tatrách. In: Výskum smrečín destabilizovaných škodlivými činiteľmi. Zvolen, Národné lesnícke centrum, p. 297–308.
- Šebeň, V., 2011b: Podiel a skladba prežívajúcej umelej obnovy na kalamitisku vo Vysokých Tatrách. In: Výskum smrečín destabilizovaných škodlivými činiteľmi. Zvolen, Národné lesnícke centrum, p. 309–321.
- Šebeň, V., Konôpka, B., Bošela, M., Pajtík, J., 2015: Contrasting development of declining and living larch-spruce stands after a disturbance event: A case study in High Tatra Mts. *Lesnícky časopis - Forestry Journal*, 61:157–166.
- Tateno, R., Hishi, T., Takeda, H., 2004: Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. *Forest Ecology and Management*, 193:297–306.
- Tobin, B., Nieuwenhuis, M., 2007: Biomass expansion factors for Sitka spruce (*Picea sitchensis* (Bong) Carr.) in Ireland. *European Journal of Forest Research* 126: 198–196.
- Vološčuk, I. et al., 1994: Tatranský národný park. Gradus, Martin, 557 p.
- Waring, R. H., Lansberg, J. J., Williams, M., 1998: Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology*, 18:129–134.
- Wirth, C., Schumacher, J., Schulze, E. D., 2004: Generic biomass functions for Norway spruce in central Europe – a meta-analysis approach toward prediction and uncertainty estimation. *Tree Physiology*, 24:121–139.
- Xiao, Ch.-W., Yuste, J. C., Janssens, I., Roskams, P., Nachtergale, L., Carrara, A. et al., 2003: Above- and belowground biomass and net primary production in a 73-year-old Scots pine forest. *Tree Physiology*, 23:505–516.
- Yuste, J. C., Konôpka, B., Janssens, I., Coenen, K., Xiao, C. W., Ceulemans, R., 2005: Contrasting net primary productivity and carbon distribution between neighbouring stands of *Quercus robur* and *Pinus sylvestris*. *Tree Physiology*, 25:701–712.
- Zianis, D., Muukkonen, P., Mäkipää, R., Mencuccini, M., 2005: Biomass and stem volume equations for tree species in Europe. *Silva Fennica*, 4:1–63.
- Zianis, D., Mencuccini, M., 2005: Aboveground net primary productivity of a beech (*Fagus moesiaca*) forest: a case study of Naousa forest, north Greece. *Tree Physiology*, 25:713–722.

Appendix

Appendix 1a. Allometric equations used for calculation of stem biomass.

Tree species	Equation	Parameters				Source
		a	b	c	λ	
<i>Acer pseudoplatanus</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-0.832	1.577	1.094	1.011	Konôpka et al. 2015
<i>Alnus incana</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-1.530	1.848	1.015	1.026	Konôpka et al. 2010
<i>Betula pendula</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-1.317	1.857	0.749	1.008	Pajtík et al. 2015a
<i>Larix decidua</i>	$B = a \cdot d^b \cdot H^c$	0.573	1.454	1.449	—	Pajtík et al. 2015b
<i>Picea abies</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-0.469	1.555	0.913	1.020	Pajtík et al. 2008
<i>Pinus sylvestris</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-0.702	1.618	0.944	1.023	Konôpka et al. 2010
<i>Populus tremula</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-0.809	1.414	1.457	1.019	Pajtík & Konôpka 2015
<i>Salix caprea</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-0.809	1.414	1.457	1.019	Pajtík & Konôpka 2015
<i>Sorbus aucuparia</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-1.317	1.857	0.749	1.008	Pajtík et al. 2015a

Appendix 1b. Allometric equations used for calculation of branch biomass.

Tree species	Equation	Parameters				Source
		a	b	c	λ	
<i>Acer pseudoplatanus</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-5.912	2.463	0.741	1.195	Konôpka et al. 2015
<i>Alnus incana</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-4.768	2.630	0.423	1.130	Konôpka et al. 2010
<i>Betula pendula</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-6.976	3.162	0.244	1.137	Pajtík et al. 2015a
<i>Larix decidua</i>	$B = a \cdot d^b \cdot H^c$	0.435	1.593	1.223	—	Pajtík et al. 2015b
<i>Picea abies</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-2.553	2.171	0.313	1.089	Pajtík et al. 2008
<i>Pinus sylvestris</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-3.184	2.232	0.310	1.066	Konôpka et al. 2010
<i>Populus tremula</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-4.569	2.605	0.275	1.079	Pajtík & Konôpka 2015
<i>Salix caprea</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-4.569	2.605	0.275	1.079	Pajtík & Konôpka 2015
<i>Sorbus aucuparia</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-6.976	3.162	0.244	1.137	Pajtík et al. 2015a

Appendix 1c. Allometric equations used for calculation of foliage biomass.

Tree species	Equation	Parameters				Source
		a	b	c	λ	
<i>Acer pseudoplatanus</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-2.626	1.941	0.008	1.082	Konôpka et al. 2015
<i>Alnus incana</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-3.286	2.188	0.188	1.100	Konôpka et al. 2010
<i>Betula pendula</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-3.389	2.240	-0.004	1.047	Pajtík et al. 2015a
<i>Larix decidua</i>	$B = a \cdot d^b \cdot H^c$	0.183	1.816	0.366	—	Pajtík et al. 2015b
<i>Picea abies</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-2.487	2.282	0.036	1.082	Pajtík et al. 2008
<i>Pinus sylvestris</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-1.901	1.993	0.024	1.089	Konôpka et al. 2010
<i>Populus tremula</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-1.939	1.803	0.290	1.061	Pajtík & Konôpka 2015
<i>Salix caprea</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-1.939	1.803	0.290	1.061	Pajtík & Konôpka 2015
<i>Sorbus aucuparia</i>	$B = e^{(a+b \cdot \ln d)^c} \lambda$	-3.389	2.240	-0.004	1.047	Pajtík et al. 2015a