

The structure of forest stands in the Tatra National Park: The results of 2016–2017 inventory

Jan Bodziarczyk¹ , Jerzy Szwagrzyk^{1*} , Tomasz Zwijacz-Kozica² , Antoni Zięba² , Janusz Szewczyk¹, Anna Gazda¹ 

¹University of Agriculture in Krakow, Faculty of Forestry, Department of Forest Biodiversity, al. 29 Listopada 46, 31-425 Kraków, Poland; ²Tatra National Park, Kuźnice 1, 34-500 Zakopane, Poland

*Tel. +48 12 66251220; +48 12 6625122; e-mail: rlbodzia@cyf-kr.edu.pl; rlszwagr@cyf-kr.edu.pl

Abstract. The composition and structure of forest stands in the Tatra National Park were examined using data gathered in 2016 and 2017 from 617 circular sample plots (0.05 ha each). The diameter at breast height of all living trees, standing dead trees, snags, and wind throws was measured along with diameters and lengths of fallen logs within the plot boundaries. Tree height was measured for all living trees within the core (0.01 ha) of the sample plots. Using the obtained data, height-diameter curves were calculated for all major tree species and in the case of spruce, the height-diameter relationships were also calculated separately for each of the three elevation zones (up to 1200 m, between 1200 and 1400 m, above 1400 m). For each elevation zone and park protection zone, we also determined the volumes of live and dead trees. The volume of living trees in the Tatra National Park amounted to 259 m³/ha, which was higher than the volume of dead trees (176 m³/ha). Snags constituted the largest part of the dead wood whilst over 97% of the standing dead trees were spruce *Picea abies*. Among living trees, the share of spruce ranged from 81% in the low elevation zone to 98% in the middle zone. Other significant species in the lower zone were *Abies alba* (11%) and *Fagus sylvatica* (4.5%), while in the middle and upper elevation zones only *Sorbus aucuparia* occurred in significant numbers. Furthermore, in the lower elevation zone, *Fagus sylvatica* was the only species displaying significantly higher volumes in the ‘strict protection’ zone compared to the other park areas. In the ‘landscape protection’ zone, *Picea abies* was the most dominant species and the share of other species in the lowest elevation zones calculated based on tree density was smaller than calculated based on tree volume, indicating problems with stand conversion from spruce monoculture to mixed forest.

Keywords: Forest vegetation belts, mountain forests, natural disturbances, stand composition

1. Introduction

The forests of the Tatra National Park (TPN) have been studied and described for a long time (Liberak 1924, Sokołowski 1936). A lot of vital information was presented in phytosociological studies published by Szafer et al. (1923, 1927), Pawłowski et al. (1928) and Horvath et al. (1980), as well as in the monographs on distribution and ecology of trees in the Tatra Mts. – prepared by the team of Prof. S. Myczkowski (1974, 1975). Much attention was also paid to the upper forest limit (Sokołowski 1928, Myczkowski 1955a) and ecology of forest communities (Myczkowski 1955b). Research by Jagiełło et al. (1978), Dziewolski et al. (1992) and Dziewolski, Skawiński (1998) provided quantitative data on the structure and species composition of the

forest stands in the Tatra Mts.; yet, the published results concerned only selected parts of this region. For overall change assessments within the region or its larger parts, including the State Treasury’s lands, there were sporadically used the results of studies based on the visual taxation method and carried out for the purposes of forest management and protection projects (Krzysztof, Mielczarek 1998). Numerous studies conducted in the Tatra forests were limited to relatively small areas, and thus, the overall picture was missing (e.g. Myczkowski 1964; Jagiełło et al. 1978; Szwagrzyk et al. 2006; Karczmarzski 1995, 2007; Modrzyński 1998; Szwagrzyk, Szewczyk 2002; Zwijacz-Kozica 2003; Holeksa et al. 2007). At the same time, the majority of the studies were conducted on subjectively selected research plots; hence, their representativeness was not adequate.

Received: 16.10.2018 r., accepted after revision: 22.03.2019 r.

Unlike other national parks designated in southern Poland, TPN lacked a network of permanent plots to monitor the status of forest stands. The first network of this kind was established in the well preserved forests of the Pieniny National Park (PPN) in the early 1970s (Dziewolski 1972) and was regularly improved in the following years, until it covered the whole Park in 2000 (Bodziarczyk et al. 2016). In the 1990s, monitoring networks were established in the Gorce National Park (Chwistek 2001), the Bieszczady National Park (Przybylska 1995; Przybylska, Kucharzyk 1999) as well as in the Babia Góra National Park (Holeksa et al. 2004), and in the next decade (after 2000) – in the Magura National Park (Sochacki 2005).

The lack of quantitative data on the structure and species composition of forest stands in TPN hindered accurate assessments of their condition and dynamics. Each of the earlier publications on forests growing in the Tatra Mts. indicated too high, in relation to site conditions, contribution of spruce (*Picea abies*) in the stands of the lower elevation zone, where this species was planted on a mass scale after extensive tree felling carried out in the 1900s – initially, for the purposes of developing mining and metallurgy industries, and later on – for needs of the wood, paper and construction industries (Sokolowski 1936; Fabijanowski 1962; Fabijanowski, Dziewolski 1996). The dominance of spruce monocultures has been already described by many authors, however, its exact quantitative dimension has remained unknown. Estimates on species dominance, performed as part of works related to forest management planning, indicated that the share of spruce in the lower elevation zone exceeded 90%, and that of fir (*Abies alba*) and beech (*Fagus sylvatica*) was just a few percent. Then, it was quite difficult to determine the effectiveness of conversion of stand species composition that was conducted within the area of TPN. The only study directly addressing this issue was based on a small number of measurement plots, and its results indicated somewhat low effectiveness of stand conversion process, and in some cases – even perpetuation of spruce dominance in the following decades (Holeksa et al. 2003).

The forests of TPN have been subject to cyclic large-area disturbances (Bzowski, Dziewolski 1973; Fabijanowski and Dziewolski 1996). For more than twenty years, a series of extreme events have been observed, including foehn winds (e.g. in 2002 and 2013) and bark beetle outbreaks (1995–1997, 2009–2013, 2016–2017) that have resulted in immense die-back of forest trees, and in particular – spruce (Sproull et al. 2017). Now, in TPN forests, there are many more gaps than 20 years ago, and thus, there occur beneficial conditions for natural regeneration. The processes of forest stand conversion may soon significantly accelerate. This is the right moment to evaluate the condition of TPN forest stands – at a time when a new generation of trees is still at the undergrowth stage. In all probability, the measurements planned in the next decade will allow to assess further tree growth and determine a rate of stand spontaneous conversion.

The aim of the present study was to demonstrate the current status of forest stands in the Tatra National Park using the statistical and mathematical methods.

2. Material and methods

2.1. Research area

The study covered the entire area of the Tatra National Park (21.1 thousand ha). The northern and central parts of TPN extend on sedimentary rocks, and the southern part constitutes the Tatra crystalline massif, built of gneisses, granodiorites and granites (Piotrowska et al., 2015). The lowest localities are characterized by a moderately cold climate (with average annual temperature and precipitation +5°C and 1100 mm, respectively). The areas situated higher than 1250 m a.s.l. have cold climate (average annual temperature and precipitation: +3°C and approx. 1400 mm, respectively), whereas those at the altitudes above 1550 m a.s.l. have very cold climate (with average annual temperature and precipitation +1°C and approx. 1700 mm, respectively) (Ustrnul et al. 2015, Żmudzka et al. 2015). The lowest localities are occupied by the Carpathian beech fertile complex *Dentario glandulosae-Fagetum*, transformed into artificially planted spruce stands on considerably large areas. Within some sites of poorer quality, there have developed fir forests *Galio-Abietetum* and fir-spruce forests *Abieti-Piceetum (montanum)* as well as marshy spruce forests *Sphagno-Piceetum* (Mirek et al. 2013). In the upper elevation zone, there dominates the West-Carpathian spruce forest association *Plagiothecio-Piceetum* and upper zone spruce forest *Polysticho-Piceetum* grows on the soils derived from limestone substrate. The areas located above the upper forest limit are covered with mountain pine *Pinetum mughi carpaticum* (Mirek et al. 2013).

2.2 Field works

Permanent research plots (500 m × 500 m) were established within the entire TPN area, with reference to the state coordinate system (Figure 1). At grid nodes, 5-are circular plots were set up and DBH measurements of all living and standing dead trees were carried out. In addition, there were measured fallen or broken trees (windthrows and snags). The heights of undamaged live trees were measured within 1-are circular plots. Within 5-are circular plots there were measured logs with the length of at least 1 m, and the thickness at the thinner end ≥ 7 cm (Szwagrzyk et al. 2016).

2.3. Data analysis

The areas with at least 1 tree (live or dead, including stumps) with DBH ≥ 7 cm were assumed as the forest areas. This way, the range of analyses also included the areas located above the upper limit of dense forest, in the zone of

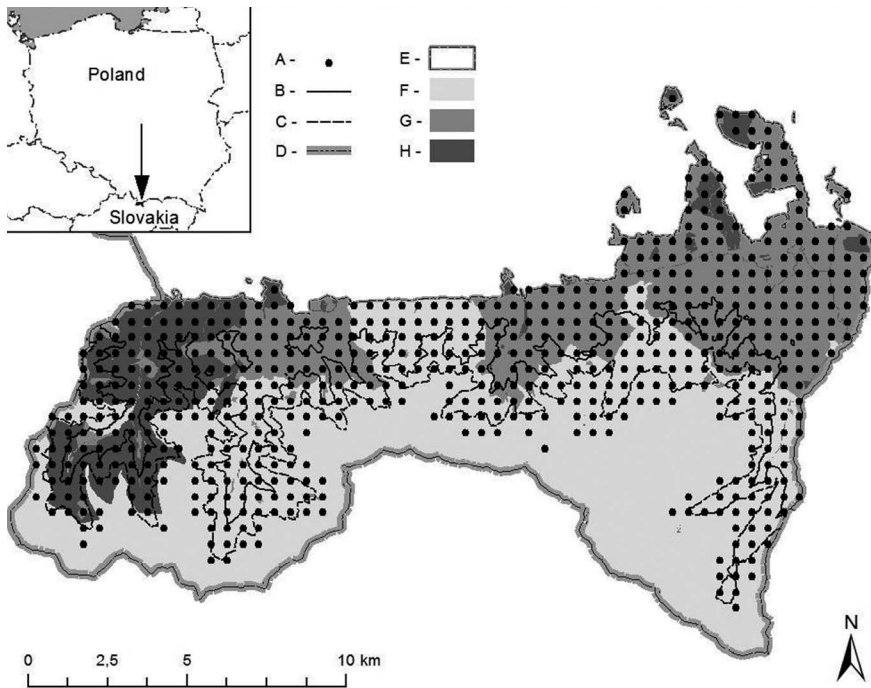


Figure 1. Distribution of permanent research plots in the Tatra National Park on the background of the various kinds of protection and altitudinal zones

Explanations:

A – permanent research plot; B – contour line 1200 m a.s.l.; C – contour line 1400 m a.s.l.; D – state border; E – borders of the Tatra National Park; F – strictly protected areas; G – active protection areas, H – areas of landscape protection

occurrence of individual trees surrounded by mountain pine forests, which – consistent with the site approach – was perceived as the site of high-mountainous coniferous forest. For the purpose of this study, in proportion to the altitudinal gradient, TPN area was divided into three notional elevation zones: lower (up to 1200 m), medium (1201–1400 m) and upper (above 1400 m), which refer to the traditional division into the lower, upper and forest upper limit zones (in the present study, these terms are used interchangeably). For each research plot, one of the three types of nature protection was assigned: strict, active, and landscape.

Based on the results of DBH and the tree height measurements carried out on live and undamaged trees, the height curves for each species were adjusted separately using Cranco program (Pommerening, 2012) and Michajłow’s formula:

$$h - a_0 \cdot e^{\frac{a_1}{DBH}} + 1.3$$

where:

h – tree height,

a_0, \dots, a_1 – regression coefficients,

DBH – tree diameter at breast height.

In the case of spruce, the relationships were described separately for the trees growing at 3 different altitudes: up to 1200 m a.s.l., 1201–1400 m a.s.l., and over 1400 m a.s.l. Then, the volume of individual trees was calculated based on DBH and the estimated tree height. The thickness of the logs was calculated using Huber’s cross-sectional formula.

Tree density and volume distributions within the research plots were analysed using the Kolmogorow-Smirnov test and the Lillefors test. The results of both tests showed that the distributions tested deviate significantly from normal distribution. For further analysis, non-parametric tests were used, that is, the Kruskal-Wallis and Chi-square tests. Statistica ver. 12 (StatSoft 2016) was used in all the tests performed.

3. Results

The average volume of live trees in the forests growing in TPN was 259 m³/ha; the share of spruce assessed based on tree volume was over 87%. The results were strongly diversified (Figure 2); therefore, detailed characteristics is presented below, broken down into the elevation zones and types of nature protection (Table 1).

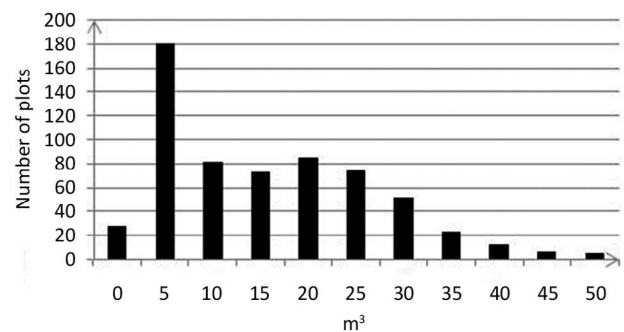


Figure 2. Distribution of wood volumes of live trees per sample plot

In the elevation zone up to 1200 m a.s.l., the average volume of live trees was slightly below 300 m³/ha, and tree density was 673 specimens/ha. The dominant species was spruce, and its share assessed based on volume (81%) was slightly higher than that assessed based on the number of trees (78%). This was even more pronounced in the case of fir, whose volume share (11%) was significantly higher than that assessed based on the number of trees (7%). Deciduous tree species showed the reverse trend (Table 1).

In the lower elevation zone, the highest average volume of live trees was observed in the Park's area under strict protection, and the smallest – in the area under landscape protection (Table 1). Analysis using the Kruskal-Wallis test showed, however, that these differences were not statistically significant. The share of beech assessed based on tree volume was by far the highest in the areas under strict protection (over 7%) – significantly higher ($H = 8.004$, $p = 0.018$) when compared to those under active and landscape protection. In the case of fir

Table 1. Average wood volume and density of living trees in various protection zones and in various elevation zones in the Tatra National Park

Species	Landscape protection		Active protection		Strict protection		TPN	
	N/ha	m ³ /ha	N/ha	m ³ /ha	N/ha	m ³ /ha	Total N/ha	Total m ³ /ha
Elevation zone up to: 1200 m a.s.l.								
<i>Abies alba</i>	51	37	48	31	48	32	48	32
<i>Acer pseudoplatanus</i>	1	0	11	2	21	5	13	3
<i>Fagus sylvatica</i>	19	9	49	6	65	23	50	14
<i>Picea abies</i>	573	228	460	247	570	253	523	242
<i>Sorbus aucuparia</i>	6	1	28	3	24	1	22	2
Total	661±586	277±228	613±484	296±240	748±626	309±202	677±567	298±223
Elevation zone: 1201–1400 m a.s.l.								
<i>Abies alba</i>	3	0	-	-	3	1	3	1
<i>Acer pseudoplatanus</i>	-	-	-	-	1	0	1	0
<i>Fagus sylvatica</i>	-	-	93	3	3	0	4	0
<i>Picea abies</i>	711	309	1200	165	754	279	753	284
<i>Sorbus aucuparia</i>	2	0	-	-	40	2	31	2
Total	716±624	310±242	1333±1357	172±117	820±638	287±229	807±650	290±230
Elevation zone: > 1400 m a.s.l.								
<i>Abies alba</i>	-	-	-	-	-	-	-	-
<i>Acer pseudoplatanus</i>	-	-	-	-	-	-	-	-
<i>Fagus sylvatica</i>	-	-	-	-	-	-	-	-
<i>Picea abies</i>	758	167	-	-	386	104	413	109
<i>Sorbus aucuparia</i>	4	0	-	-	34	4	32	3
Total	782±837	181±186	-	-	437±465	114±144	462±504	119±147
All elevation zones together								
<i>Abies alba</i>	30	21	47	31	17	11	26	17
<i>Acer pseudoplatanus</i>	1	0	10	2	7	2	7	1
<i>Fagus sylvatica</i>	11	5	50	6	23	8	27	7
<i>Picea abies</i>	635	251	477	245	578	216	567	228
<i>Sorbus aucuparia</i>	5	0	27	3	33	2	27	2
Total	690±617	280±231	630±520	294±239	677±607	241±214	670±591	259±223

and sycamore (*Acer pseudoplatanus*), the differences were not statistically significant; the volume share of fir was the largest in the area under landscape protection (13%), and the smallest – in the area under strict protection. In the case of sycamore, the relatively largest share (over 1%) was observed in the area under strict protection (Table 1). In the lower elevation zone, the landscape protection area was the only one where the share of spruce assessed based on the number of trees (87%) was lower than that assessed based on tree volume (82%). In the areas under strict and active protection, there were observed opposite relationships (Table 1). Among the tree species analysed, fir was the only one whose share assessed based on the number of trees was in each case lower when compared to that assessed based on tree volume (Table 1). In the elevation zone 1201 m–1400 m a.s.l., the share of spruce assessed based on tree volume was almost 99%. In the area under strict protection, mountain-ash (*Sorbus aucuparia*) constituted a relatively large admixture, reaching the share 0.9% when assessed based on tree volume and 4.8% when assessed based on the number of trees (Table 1). In the area under strict protection, there was also observed a trace share of larch (*Larix* sp.) and Swiss pine (*Pinus cembra*). At the same time, the volume of live trees in the elevation zone 1200 m–1400 m was evidently lower than that observed in the lower elevation zone (below 1200 a.s.l.) (Table 1).

In the elevation zone above 1400 m a.s.l., in the area under strict protection, both tree density (462 specimen/ha) and the volume of live trees (119 m³/ha) were comparatively lower. However, the share of admixture species was significantly higher – 4.6% and 3.2% of Swiss pine and mountain-ash, respectively.

The analysis of relationship between stand volumes and elevations above sea level was carried out only for trees growing in the area under strict protection, with appropriate representation of all the elevation zones. Significant ($p < 0.001$) differences were found in the volume of live trees between the upper forest limit zone and the lower and upper elevation zones, and the difference between the two latter elevations was not significant (Figure 3). Likewise, significant differences ($p < 0.001$) were also observed in the case of the volume of living spruce trees between elevation zones.

The average volume of dead wood was 180 m³/ha, that is, slightly higher than $\frac{2}{3}$ of the volume of live trees. Snag volume was the highest and that of windthrows was the lowest (Table 2). In the elevation zone below 1200 m a.s.l., in the areas under strict protection, the volume of dead wood was on average almost 243 m³/ha – significantly the highest (Kruskal-Wallis test). In the area under strict protection, dead wood volume in 1200 m–1400 m elevation zone was slightly higher (248 m³/ha) than that in the zone below 1200 m a.s.l., whereas in the elevation zone above 1400 m a.s.l., dead wood volume amounted to 110 m³/ha (Table 2). Differences between stands growing in the elevation zones below and above 1400 m a.s.l. were statistical-

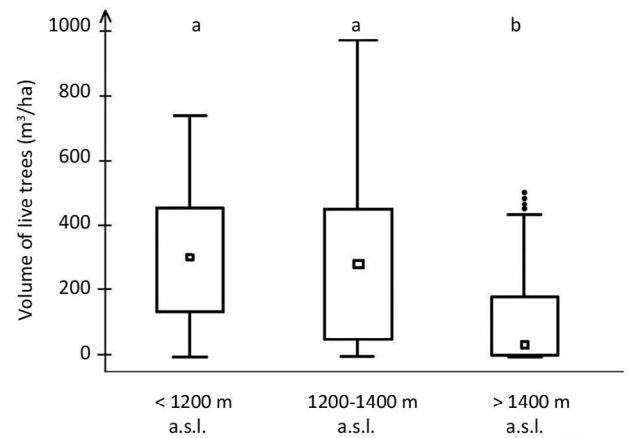


Figure 3. Volume of living trees in three elevation zones in the area under strict protection

Explanations:

a – statistically non-significant difference;

b – statistically significant difference

ly significant ($p < 0.001$), and no significant differences were found between forests growing in the elevation zone below 1200 m and those growing at the altitude 1200 m–1400 m a.s.l. Spruce constituted over 97% of the total dead wood volume.

4. Discussion

The average forest stand volume in the Tatra National Park is currently somewhat lower than that in forests growing in the Polish part of the Carpathian Mountains – estimated as 321 m³/ha (WISL 2015). It is also much lower than the average stand volumes estimated in Poland's other national parks, for example, in the Babia Góra National Park – 400 m³/ha (Holeksa et al. 2004), in the Gorce National Park – 403 m³/ha (Chwistek et al. 2018), in the Pieniny National Park – 475 m³/ha (Operat 2010), and in the Bieszczady National Park – 354 m³/ha (Przybylska, Kucharzyk 2016). In the case of TPN, comparatively lower stand volume values are largely due to the impact of climatic factors associated with the elevation above sea level. In the present study, the influence of climate is well illustrated by decreasing stand volumes observed in the areas under strict protection; in the zone up to 1200 m a.s.l., the stand volume reaches 318 m³/ha, whereas in the elevation zone 1400 m a.s.l., it amounts to no more than 102 m³/ha. In the Polish part of the Carpathians, the Tatra Mts. are covered with a larger area of forests growing at higher altitudes when compared to the other Poland's national parks, and this considerably affects the average stand volume in the region.

Nonetheless, natural disturbances, such as strong winds and bark beetle outbreaks play a key role in shaping forest stand

Table 2. Average dead wood volume (\pm SD) in various protection zones and in various elevation zones in the Tatra National Park

Elevation zone	Dead trees	Landscape protection	Active protection	Strict protection	TPN Total
		m ³ /ha			
< 1200 m a.s.l.	Standing deadtrees	14	13	31	21
	Snags	111	64	118	95
	Windthrows	23	17	42	28
	Logs	8	25	51	32
	Total	154	119	243	176
1200–1400 m a.s.l.	Standing deadtrees	26	1	50	44
	Snags	120	46	125	122
	Windthrows	13	-	24	21
	Logs	17	1	49	41
	Total	175	48	248	229
>1400 m a.s.l.	Standing deadtrees	22	-	26	26
	Snags	173	-	44	53
	Windthrows	45	-	11	13
	Logs	20	-	29	28
	Total	260	-	110	120
TPN Total	Standing deadtrees	18	13	36	28 \pm 68
	Snags	119	64	98	94 \pm 139
	Windthrows	21	16	26	23 \pm 63
	Logs	12	25	43	34 \pm 71
	Total	170	117	203	180 \pm 229

volumes in the Tatra Mts., which is confirmed by the observed accumulation of dead wood. Currently, the average volume of dead wood in TPN forests exceeds that in other protected areas designated in Poland, such as the Babia Góra National Park, where the average dead wood volume is 19 m³/ha (Holeksa et al. 2004), the Pieniny National Park – 55 m³/ha (Operat 2010), and the Bieszczady National Park – 58 m³/ha (Przybylska, Kucharzyk 2016). Evidently, in TPN, prevalent accumulation of dead wood occurs in strictly protected areas; yet, it is worth noting that also in the areas under active and landscape protection, dead wood volumes reach the levels comparable with the strict protection areas of other national parks in Poland and greatly exceed dead wood volumes in the managed forests (Czerepko 2008). The majority of dead wood in TPN comprises not yet decomposed dead trees, damaged due to foehn winds and bark beetle outbreaks. Nevertheless, as some forests in TPN are classified as close to natural (Karczmarski, 1995; Szwagrzyk, Szewczyk 2002), and their dead wood resources have preserved temporal and spatial continuity (Szwagrzyk et

al. 2006), organisms associated with dead wood have a great opportunity to colonize numerous dead trees that have emerged in TPN in the recent decades.

The average values obtained show very wide confidence intervals, and the coefficients of variation as a general rule exceed 100%. These values are distinctly higher than those estimated in the managed forests (WISL 2015) or in the Bieszczady National Park (Kucharzyk, Przybylska 1998). It is worth noting that the number of trial plots set up in TPN (617) was comparable to those established in the other national parks of southern Poland, such as: the Bieszczady National Park – 910 (Kucharzyk, Przybylska 1998), the Gorce National Park – 400 (Chwistek 2001) or the Pieniny National Park – 374 (Operat 2010). The number of plots in the Tatra forests reflects huge spatial variability in the region. No data is available on spatial variability of TPN forests in an earlier period, but their current status is undeniably a result of natural disturbances – winds and bark beetle outbreaks. Contrary to intuitive evaluations, natural disturbances do not cause homogenization of the forest structure and landscape, but

greatly increase forest spatial diversity (Turner 2010). Standard practices undertaken by foresters to repair damage done by natural disturbances, for example, removing dead and damaged trees and planting new forests (Foster, Orwig 2006) lead to the standardization of tree stands. Conversely, in TPN, even in the areas under active protection, human interference after disturbances is limited to a great extent; hence, stand conversion is principally carried out in a natural way.

The share of spruce in forests growing in the lower elevation zone is still very high, even if taking into account the fact that a part of these encompass the communities of fir-spruce forests *Abieti-Piceetum (montanum)* and the West-Carpathian spruce forest association *Plagiothecio-Piceetum* descending on moraine tracks down into the lower elevation zone (Piękna-Mirkowa, Mirek, 1996). Furthermore, the share of spruce in close to natural beech stands amounts to about 20% (Szwagrzyk et al. 2006). The present status is to a large extent a reflection of forest management in the past, when spruce was the preferred species used in reforestation for over a hundred years (Sokołowski 1936; Fabijanowski 1962).

In beech forests, there are evident progressing stand conversion processes in the Park areas under active protection as well as spontaneous changes in the areas under strict protection. Now, in the lower elevation zone, beech shows a larger share when assessed based on the number of trees when compared to that assessed based on the stand volume. Similar tendencies are obvious in the case of sycamore and mountain-ash. The status of fir is worse; it seems that regeneration of this species going on in the last decades in forests growing in the lower elevation zone does not guarantee either maintaining the present share of fir or its increasing. This trend is opposite to that just observed in the forests of the Babia Góra National Park (Holeksa et al. 2004) or the Gorce National Park (Chwistek 2001). Perhaps the trend observed in TPN will change, as the latest data on grazing young tree regeneration (Bodziarczyk et al. 2017) show low levels of fir grazing by ungulates.

In TPN, the area under landscape protection is quite alarming, as the share of spruce in forests in the lower elevation zone is comparatively the highest, and conversion of species composition has not so far showed any significant progress. The current status of growing here forests, with numerous gaps and large areas covered by heavily ‘thinned out’ stands, provides opportunities to accelerate the conversion process; however, this will not be easy, because in this area, spruce has remained the tree species with the greatest seeding capacity.

Considering the large share of dead trees in the forests of TPN and the fact that spruce constitutes about 97% of the total dead wood amount, it should be noted that the share of this species has notably decreased in the last decades – from over 91% to 88%. As conversion of stand species composition has been intentionally carried out neither in the higher elevation zone nor in the upper forest limit zone, a meaningful compa-

rison is possible as regards the lower elevation zone. In the past, the estimated share of spruce in forests growing in the lower elevation zone was about 89%. Now, in the elevation zone below 1200 m a.s.l., the share of live spruce trees is 81%. The decrease of spruce share by about 8% in the last decades has not been a great success in conversion of low elevation forest stands, but it is certainly a step in the right direction.

Conflict of interest.

The authors declare the lack of potential conflicts.

Acknowledgements and source of funding

In 2016, the study was financed by the Tatra National Park thanks to the funds obtained from the Forest Fund established



Figure 4. Well preserved spruce forest stand in upper montane zone in strictly protected area (plot no. 678)

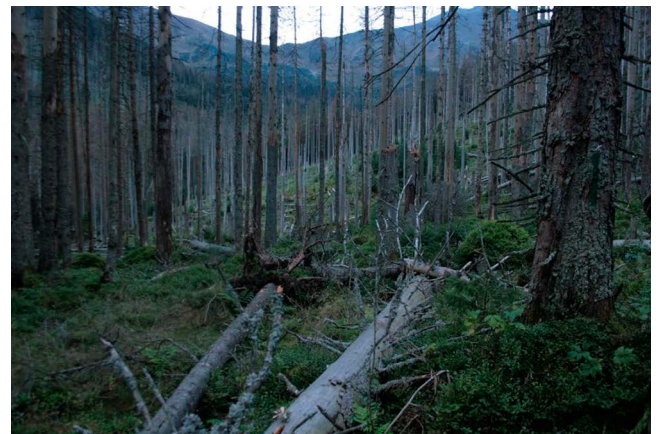


Figure 5. Spruce stand forest influenced by severe natural disturbance in upper montane zone in strictly protected area (plot no. 135)

by the State Forests National Forest Holding, and in 2017 – from own financial resources of TPN. Additionally, it was financed from a subsidy granted by the Ministry of Science and Higher Education to the statutory activities of the Department of Forest Biodiversity, Faculty of Forestry, University of Agriculture in Kraków (grant No. DS 3421/ ZBL).

References

- Bodziarczyk J., Pancer-Koteja E., Różański W. 2016. Charakterystyka leśnej szaty roślinnej Pienińskiego Parku Narodowego na podstawie systematyczno-losowej próby danych. *Pieniny – Przyroda i Człowiek* 14: 17–50. ISSN 1230–4751.
- Bodziarczyk J., Zwijacz-Kozica T., Gazda A., Szewczyk J., Frączek M., Zięba A., Szwagrzyk J. 2017. Skład gatunkowy, wzniesienie nad poziomem morza i kategoria ochrony jako czynniki wpływające na intensywność zgrzyzania odnowień w Tatrzańskim Parku Narodowym. *Leśne Prace Badawcze* 78(3): 238–247. DOI 10.1515/frp-2017-0026.
- Bzowski M., Dziewolski J. 1973. Zniszczenia w lasach Tatrzańskiego Parku Narodowego spowodowane przez wiatr halny wiosną 1968 r. *Ochrona Przyrody* 38: 115–154.
- Chwistek K., Loch J., Czarnota P., Armatus P. 2018. Monitoring drzewostanów Gorczańskiego Parku Narodowego. Manuskrypt.
- Chwistek K. 2001. Dynamics of tree stands in the Gorce National Park during the period 1992–1997. *Nature Conservation* 58: 17–32. ISSN 1643-9252.
- Czerepko J. (red.) 2008. Stan różnorodności biologicznej lasów w Polsce na podstawie powierzchni obserwacyjnych monitoringu. Synteza wyników uzyskanych w ramach realizacji projektu BioSoil Forest Biodiversity. Instytut Badawczy Leśnictwa, Sękocin Stary. ISBN 978-83-87647-75-9.
- Dziewolski J. 1972. Naturalne zmiany struktury wybranych drzewostanów Pienińskiego Parku Narodowego w okresie 32 lat (1936–1968). *Ochrona Przyrody* 37: 263–283.
- Dziewolski J., Holeksa J., Skawiński P. 1992. Przemiany dolnoregłowych drzewostanów Tatrzańskiego Parku Narodowego w latach 1956–1986 oraz ocena metod ich przebudowy. *Ochrona Przyrody* 50: 95–108. ISSN 0078-3250.
- Dziewolski J., Skawiński P. 1988. Zmiany w składzie gatunkowym i strukturze wiekowej wybranych drzewostanów Tatrzańskiego Parku Narodowego. *Ochrona Przyrody* 46: 75–90. ISBN 83-01-07841-3.
- Fabijanowski J. 1962. Lasy Tatrzańskie, w: Tatrzański Park Narodowy (red. W. Szafer). Kraków, PAN, Zakład Ochrony Przyrody, 240–304.
- Fabijanowski J., Dziewolski J. 1996. Gospodarka leśna, w: Przyroda Tatrzańskiego Parku Narodowego (red. Z. Mirek). Tatrzański Park Narodowy, Instytut Botaniki PAN, Instytut Ochrony Przyrody PAN, Zakopane-Kraków, 655–696. ISBN: 83-85832-08-4.
- Foster D.R., Orwig D. 2006. Preemptive and Salvage Harvesting of New England Forests: When Doing Nothing is a Viable Alternative? *Conservation Biology* 20(4): 959–970. DOI:10.1111/j.1523-1739.2006.00495.x
- Holeksa J., Greinert J., Krzan Z., Olszowska B., Skawiński P., Wika S. 2003. Przemiany dolnoregłowych drzewostanów świerkowych poddanych ochronie częściowej w Tatrzańskim Parku Narodowym. *Sylvan* 147(10): 37–46. ISSN 0039-760.
- Holeksa J., Szwagrzyk J., Musiałowicz W., Parusel J.B. 2004. Struktura i dynamika lasów Babiogórskiego Parku Narodowego, w: Babiogórski Park Narodowy (red. B.W. Wołoszyn, A. Jaworski, J. Szwagrzyk). Monografia Przyrodnicza. Babiogórski Park Narodowy. Komitet Ochrony Przyrody PAN. Kraków, 528–598. ISBN 83-89707-39-X.
- Holeksa J., Krawczyk B., Skawiński P., Wesołowska M., Wika S. 2007. Zmiany górnoeregłowego drzewostanu świerkowego w Tatrzańskim Parku Narodowym w latach 1973–2002. *Sylvan* 151(9): 29–40. ISSN 0039-760.
- Horvath I., Bretović S., Pawłowski B., Pawłowska S., Zarzycki K. Z. 1980. Mapa fitosocjologiczna Sarniej Skały w Tatrach Zachodnich (rok 1958). *Ochrona Przyrody* 43: 75–90. ISBN 83-01-01386-9.
- Jagiello Z., Poznański R., Raimer J., Rutkowski B. 1978. Zastosowanie wielkoobszarowej metody losowych powierzchni próbnych do inwentaryzacji i kontroli zapasu i przyrostu w projektowanym rezerwacie ścisłym Skoruśniak w Tatrzańskim Parku Narodowym. *Sylvan* 122(1): 31–41.
- Karczmarski J. 1995. Budowa i struktura tatrzańskich górnoeregłowych borów świerkowych o charakterze pierwotnym w dolinach Rybiego Potoku, Pańszczyicy i Gąsienicowej. *Acta Agraria et Silvicultura, Series Silvestris* 33: 167–198. ISSN 0065-09227.
- Karczmarski J. 2007. Budowa, struktura i dynamika górnoeregłowych borów świerkowych o charakterze pierwotnym w dolinach Pańszczyicy i Stawów Gąsienicowych (Tatrzański Park Narodowy) w okresie kontrolnym 1991–2002. *Sylvan* 11: 41–59. ISSN 0039-760.
- Krzan Z., Mielczarek S. 1998. Zmiany składu gatunkowego i struktury wiekowej świerczyny Tatrzańskiego Parku Narodowego w dwudziestolecie 1975–1994. *Zeszyty Naukowe Akademii Rolniczej w Krakowie. Leśnictwo* 332(56): 111–121. ISSN 0239-9342.
- Lasy Państwowe w liczbach 2017. Centrum Informacyjne Lasów Państwowych. Warszawa. ISBN 978-83-65659-24-8.
- Liberak M.A. 1924. Kornik w lasach polskich Tatr. Nakładem Związku Podhalańskiego w Nowym Targu. Zakopane, 34 s.
- Mirek Z., Jaworski A., Holeksa J., Czerny M., Krawiec A., Mroczek K., Szmalec T., Łaptos J., Myjak P., Mitka K., Bodzioch R., Lomber J. 2013. Operat ochrony ekosystemów leśnych i zaroślowych TPN. Manuskrypt.
- Modrzyński J. 1998. Dendrometryczna i morfologiczna charakterystyka drzewostanów świerkowych położonych na różnych wysokościach nad poziomem morza w Tatrach. *Zeszyty Naukowe Akademii Rolniczej w Krakowie* 332(56): 97–109. ISSN 0239-9342.
- Myczkowski S. 1955a. Naturalne szpalery świerkowe nad górną granicą lasu na stokach Małej Kosistej w Tatrach. *Chrońmy Przyrodę Ojczystą* 11(2): 22–27.
- Myczkowski S. 1955b. Ekologia zespołów leśnych Tatr Polskich ze szczególnym uwzględnieniem jej związku z pokrywą śnieżną. *Ochrona Przyrody* 23: 112–203.

- Myczkowski S. 1964. Struktura i ekologia zespołu świerka *Picea-tatricum* u górnej granicy zasięgu w Tatrzańskim Parku Narodowym w dolinach Stawów Gąsienicowych i Pańszczycy. *Ochrona Przyrody* 30: 51–105.
- Myczkowski S. (red.) 1974. Rodzime drzewa Tatr. Studia Ośrodka Dokumentacji Fizjograficznej, tom III. Wydawnictwo PAN, Kraków, 1–200.
- Myczkowski S. (red.) 1975. Rodzime drzewa Tatr. Studia Ośrodka Dokumentacji Fizjograficznej, tom IV. Wydawnictwo PAN, Kraków, 1–304.
- Operat 2010. Operat ekosystemów leśnych 2010. Dokumentacja do Planu Ochrony Pienińskiego Parku Narodowego na lata 2011–2030. Manuskrypt.
- Pawłowski B., Sokołowski M., Wallish K. 1928. Zespoły roślin w Tatrach. cz. 7. Zespoły roślinne i flora doliny Morskiego Oka. *Rozprawy Wydziału Matematyczno-Przyrodniczego PAU* 6, A/B: 171–311.
- Piękoś-Mirkowa H., Mirek Z. 1996. Zbiorowiska roślinne, w: *Przyroda Tatrzańskiego Parku Narodowego* (red. Z. Mirek). Kraków-Zakopane. Tatrzański Park Narodowy, 237–274. ISBN: 83-85832-08-4.
- Piotrowska K., Danel W., Iwanow A., Gaździcka E., Rączkowski W., Bezák V., Maglay J., Polák M., Kohút M., Gross P. 2015. Budowa geologiczna. Atlas Tatr. *Przyroda nieożywiona: IV.1*. ISBN 978-83-61788-91-1.
- Pommerening A. 2012. Crancod, A Program for the Analysis and Reconstruction of Spatial Forest Structure. Version 1.4.
- Przybylska K. 1995. Monitorowanie procesów zachodzących w drzewostanach Bieszczadzkiego Parku Narodowego. *Roczniki Bieszczadzkie* 4: 254–255. ISBN 83-86994-30-4.
- Przybylska K., Kucharzyk S. 1999. Skład gatunkowy i struktura lasów Bieszczadzkiego Parku Narodowego. *Monografie Bieszczadzkie* 6: 1–159. ISBN 83-903209-9-1.
- Przybylska K., Kucharzyk S. 2016. Skład gatunkowy i struktura lasów BdPN, w: *Bieszczadzki Park Narodowy – 40 lat ochrony* (red. A. Górecki, B. Zemanek), Ustrzyki Górne, 117–128. ISBN 978-83-88505-53-9.
- Sochacki J. 2005. Monitoring naturalnych drzewostanów Magurskiego Parku Narodowego. *Magurski Park Narodowy, Krempna*, Manuskrypt, 58 s.
- Sokołowski M. 1928. O górnej granicy lasu w Tatrach. Wydawnictwo Fundacji Zakłady Kórnickie, Kraków, 188 s.
- Sokołowski S. 1936. Las tatrzański. *Z Tatr i Podhala* 2: 1–136.
- Sproull G.J., Bukowski M., McNutt N., Zwijacz-Kozica T., Szwagrzyk J. 2017. Landscape-level spruce mortality patterns and topographic forecasters of bark beetle outbreaks in managed and unmanaged forests of the Tatra Mountains. *Polish Journal of Ecology* 65(1): 24–37. DOI 10.3161/15052249PJE2017.65.1.003.
- StatSoft Inc. 2016. Statistica (data analysis soft-ware system), version 12. www.statsoft.com.
- Szafer W., Pawłowski B., Kulczyński S. 1923. Die Pflanzenassoziationen des Tatra-Gebirges. I Teil. Die Pflanzenassoziationen des Chochołowska Tales. *Bulletin International de l'Académie Polonaise des Sciences et des Lettres, Classe des Sciences Mathématiques et Naturelles, Serie B, Numéro supplémentaire* 3: 1–66.
- Szafer W., Pawłowski B., Kulczyński S. 1927. Die Pflanzenassoziationen des Tatra-Gebirges. III Teil. Die Pflanzenassoziationen des Kościeliska Tales. *Bulletin International de l'Académie Polonaise des Sciences et des Lettres, Classe des Sciences Mathématiques et Naturelles, Serie B, Numéro supplémentaire* 2: 13–78.
- Szwagrzyk J., Bodziarczyk J., Gazda A., Szewczyk J. 2016. Budowa i struktura tatrzańskich drzewostanów na podstawie regularnej siatki powierzchni próbnych. Etap 1 – Tatry Zachodnie. Raport, Tatrzański Park Narodowy, 33 s.
- Szwagrzyk J., Sulowski W., Skrzydłowski T. 2006. Struktura naturalnego drzewostanu buczyny karpackiej w Tatrach na tle naturalnych buczyn z innych masywów Karpat. *Sylwan* 150(9): 3–15. ISSN 0039-760.
- Szwagrzyk J., Szewczyk J. 2002. Przestrzenne różnicowanie struktury wiekowej populacji świerka w drzewostanach górnoregłowych tatrzańskiego Parku Narodowego, w: *Przemiany środowiska przyrodniczego Tatr* (red. W. Borowiec, A. Kotarba, A. Kownacki, Z. Krzan, Z. Mirek). Kraków-Zakopane, 229–232. ISBN 83-85832-42-4.
- Turner M.G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91(10): 2833–2849. DOI: 10.1890/10-0097.1.
- Ustrnul Z., Waławender E., Czekierda D., Šťastný P., Lapin M., Mikulová K. 2015. Opady atmosferyczne i pokrywa śnieżna. Atlas Tatr. *Przyroda nieożywiona: II.3*. ISBN 978-83-61788-91-1.
- WISL 2015. Wielkoobszarowa Inwentaryzacja Stanu Lasu. Wyniki II cyklu (lata 2010-2014). Praca wykonana przez Biuro Urządzenia Lasu i Geodezji Leśnej na zamówienie Dyrekcji Generalnej Lasów Państwowych. Państwowe Gospodarstwo Leśne Lasy Państwowe. Sękocin Stary, 176 s.
- Zwijacz-Kozica T. 2003. Różnicowanie się struktury populacji świerka w procesie starzenia tatrzańskich borów górnoregłowych. Rozprawa doktorska. SGGW, Warszawa.
- Žmudzka E., Nejedlík P., Mikulová K. 2015. Temperatura, wskaźniki termiczne. Atlas Tatr. *Przyroda nieożywiona: II.2*. ISBN 978-83-61788-91-1.

Authors' contribution

J.B. – research concept, coordination of field data collection, calculations, manuscript writing/revising; J.Szwa. – research concept, manuscript writing/revising; T.Z-K. – research concept, field data collection, manuscript writing/revising; A.Z. – field data collection, manuscript writing; J.Sze. – setting up database; A.G. – calculations, data statistical analysis, manuscript writing.