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Authors: Zięba, Antoni, Różański, Wojciech, and Szwagrzyk, Jerzy

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Structure of dominance among tree species in relic Swiss stone pine (*Pinus cembra* L.) forests in Tatra Mountains

Antoni ZIĘBA[1]*, Wojciech RÓŻAŃSKI[2] and Jerzy SZWAGRZYK[2]

[1]Tatra National Park, ul. Kuźnice 1, 34-500 Zakopane, Poland, Department of Forest Biodiversity, University of Agriculture in Kraków, al. 29 listopada 46, 31-425 Kraków, Poland; *e-mail: azieba@tpn.pl (corresponding author)

[2]Department of Forest Biodiversity, University of Agriculture in Kraków, al. 29 listopada 46, 31-425 Kraków, Poland

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ABSTRACT

Pinus cembra forests are limited to the Alps and Carpathians. Although several studies regarding their structure were carried out in some locations in the Tatra Mts. it required further investigations. Therefore, the aims of this study were to describe the stand and shrub structure of *P. cembra* forests, compare their structure with the *Picea abies* forests and analyse differences between silicate and calcicolous *P. cembra* forests in the Tatra Mts. The data were collected on the 16 sampling plots (500 m^2), in the Swiss stone pine and Norway spruce forests. We measured the diameter at breast height (dbh) of each tree and recorded the young trees and shrubs. In order to compare species composition between silicate and calcicolous *P. cembra* forests, we made 91 relevés in their entire range of distribution (917 ha). Furthermore, we examined the share of main tree species along the altitude and inclination gradients, using the GAM models. The tree density in the *P. cembra* forests reaches 618 stems per ha, whereas their basal area (BA) 23.17 m^2 ha^{-1}. Main tree species are *P. cembra* and *P. abies*. *P. cembra* dominates in the higher thickness classes. The BA and dbh structure varies significantly between *P. cembra* and *P. abies* forests. The most abundant juveniles are *P. abies* and *Sorbus aucuparia*. The differences between forests growing on different substrate are relatively low. The altitude has a significant impact on the share of *P. cembra* (increase) and *P. abies* (decrease). The inclination has a significant impact on the increase of share of *P. cembra*.

INTRODUCTION

Swiss stone pine (*Pinus cembra*) grows naturally only in Europe. Its distribution is limited to the Alps and higher parts of the Carpathian Mountains. This tree forms mixed stands with European larch (*Larix decidua*), Norway spruce (*Picea abies*) and admixture of deciduous montane trees (Ellenberg 1978, Caudullo and de Rigo 2016, Leuschner and Ellenberg 2017). According to some authors these forests are relics of first woodlands that occurred in the Central Europe at the transition between Pleistocene and Holocene (Szafer 1966, Bednarz 1969, Obidowicz *et al.* 2004). Swiss stone pine forests represent high conservation values due to their complex structure, ecology and limited distribution as well as protection of alpine areas against the natural hazards (Brang *et al.* 2006, Leuschner and Ellenberg 2017). Some of them represent well-preserved old-growth forests in Europe (Ellenberg 1978, Zielonka 2010, Ballmer *et al.* 2014, Leuschner and Ellenberg 2017, Popa *et al.* 2017).

Studies on *P. cembra* forests in the Tatra Mts. were initiated in the 1960/70's (Myczkowski 1969, 1971, Myczkowski and Bednarz

1974,). Since then, several studies on ecology of these forests were carried out (Jamnický 1981, Wojterska *et al.* 2004, Zwijacz-Kozica and Żywiec 2007, Kanka 2008, Zwijacz-Kozica *et al.* 2010, Valachovič 2014, Zięba *et al.* 2019). Swiss stone pine forests in the Tatra Mts. form two different plant associations: *Vaccinio-Pinetum cembrae* – on granite, and *Swertio perennis-Pinetum cembrae* – on limestone (Zięba *et al.* 2018). They occur mostly at the elevation 1300–1650 m a.s.l. and prefer steep (average inclination: 27°) western slopes. Even though they may grow on rich Rendzic Leptosols, they occur mostly on Podzols (Zięba *et al.* 2019). Due to inaccessibility of these forests some of their parts stayed untouched and can be claimed as virgin forests (Bednarz 1969, Zielonka 2010, Zięba *et al.* 2018). Swiss stone pines reach there even 300–500 years (Jamnický 1981, Zielonka 2010).

Several studies concerning the structure of the *P. cembra* forests were conducted in the Alps and in the Southern and Eastern Carpathians (Risch *et al.* 2003, Motta and Lingua 2005, Ballmer *et al.* 2014, Giammarchi *et al.* 2017, Popa *et al* 2017, Beloiu and Beierkuhnlein 2019). Mean basal area of these forests in the Alps and Carpathians varies between *ca* 20÷50 m^2 ha^{-1}. The stands in the Alps consist of majority of *P. cembra* and *L. decidua*, whereas in the Carpathians *P. abies* seems to replace European larch (Risch *et al.* 2003, Motta and Lingua 2005, Ballmer *et al.* 2014, Giammarchi *et al.* 2017, Popa *et al* 2017).

Although the state of knowledge regarding these forests in the Tatra Mts. has increased recently, the cognition of the structure of *P. cembra* stands was still very limited. The most comprehensive study concerning this issue was made by Vološčuk (2012) in the southern side of these mountains (Slovakia). Remaining studies mostly represented spruce forests with admixture of *P. cembra* rather than pure or dominated by Swiss stone pine stands (Korpel 1989, Voško 1995, Zwijacz-Kozica and Żywiec 2007). They were also limited to relatively small areas. Therefore, the main aim of this work was to describe the structure of *P. cembra* forests in the Tatra Mts.

Furthermore, Swiss stone pine forests in the Tatra Mts. were considered for a long time as a variant of upper montane spruce forests (Matuszkiewicz 2008, Mróz *et al.* 2012). Recent studies confirmed that they form separate plant communities from the *P. abies* forests and occupy slightly different habitats (Zięba *et al.* 2018, 2019). However, the differences in stand structure between these two types of forests were not investigated. Therefore, we wanted to check whether their structure varies just as a floristic composition and site properties or it is similar.

Moreover, stands with *P. cembra* in the Tatra Mts. were considered for a long time as limited to the silicate part of these mountains (Holeksa and Szwagrzyk 2004, Matuszkiewicz 2008, Mróz *et al.* 2012). However, the results of recent studies pointed out their occurrence on the limestones and dolomites (Kanka 2008, Kučera 2017, 2018, Zięba *et al.* 2018, 2019). Calcicolous *P. cembra* forests in the Tatra Mts. occur on much smaller area than those on silicate bedrock and floristically they vary considerably (Zięba *et al.* 2018, 2019). We wanted to check the differences in stand and shrub layer of these two types of Swiss stone pine forests.

In addition to this, studies on habitat requirements of *P. cembra* forests in the Tatra Mts. showed that the probability of occurrence of these forests increases along the altitude (up to 1700 m a.s.l.) and inclination gradients (Zięba *et al.* 2019). We would like to investigate how these dependencies are expressed at the stand level. Therefore, we analysed the changes in the share of main tree species: *P. cembra* and *P. abies* along altitude and inclination gradients.

STUDY AREA

The Tatra Mts. are the highest mountains in the Carpathians (highest peak: Gerlach ÷ 2655 m a.s.l.). They are located at the border of Poland and Slovakia (Fig. 1). Due to the different geomorphology, flora and elevation they are divided into three parts: Western Tatra Mts., High Tatra Mts. and Belianske Tatra Mts. (Balon *et al.* 2015). Even though their total area is just *ca* 790 km^2 they represent very high level of biodiversity, including many endemic species of plants and animals (Mirek 1996, Šoltesova *et al.* 2010). Because of high environmental values, they are pro-

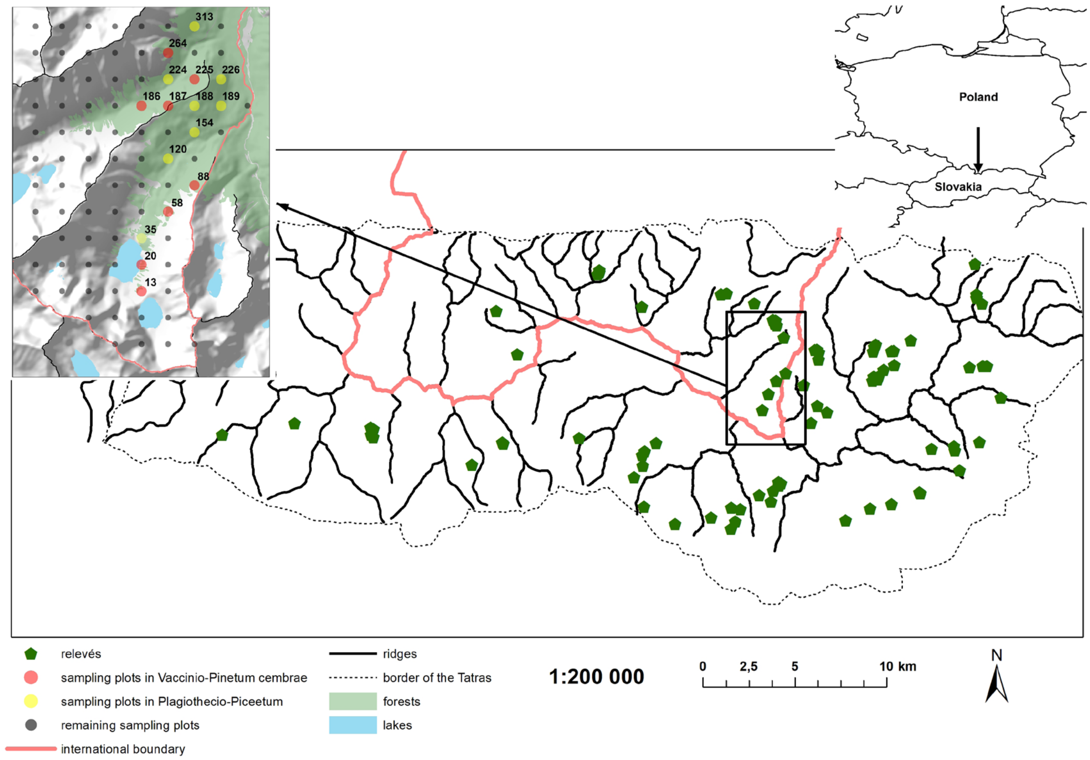

Fig. 1. Location of sixteen permanent sampling plots in the Swiss stone pine forests (*Vaccinio-Pinetum cembrae*) and Norway spruce forests (*Plagiothecio-Piceetum*) (upper left corner) and 91 relevés collected in the entire distribution of *Pinus cembra* forests in the Tatra Mts. (centre).

tected on both Polish and Slovakian side by National Parks (Mirek 1996).

The study was carried out in the entire range of *P. cembra* forests (917 ha) (Zięba *et al.* 2019). Swiss stone pine forests grow in the zone of cool climate with mean annual temperature of +3°C and mean annual sum of precipitation of 1400 mm (Hess 1996, Ustrnul *et al.* 2015, Żmudzka *et al.* 2015). Snow cover lasts in these subalpine forests for *ca* 150 days/year (Ustrnul *et al.* 2015).

MATERIAL AND METHODS

Data collection

We used two approaches of data collection. The data on the stand structure, such as thickness, basal area (BA) and tree density were collected in regularly distributed (500 × 500 m) circular sample plots (500 m^2 each) in the Polish Tatra National Park (TNP) (Bodziarczyk *et al.* 2019). We collected data on eight circular plots representing Swiss stone pine forests (*Vaccinio-Pinetum cembrae*) and on eight neighbouring plots in the Norway spruce forests (*Plagiothecio-Piceetum*). All of the plots are located in the Białka Valley in the High Tatra Mts., in the strict conservation zone and represent natural, mature and recently undisturbed patches of forests. Plots representing *P. cembra* forests were situated at the elevation 1233–1530 m a.sl., whereas those in *P. abies* forests at 1192–1418 m (Fig. 1). The entire area is build out of granites or glacial moraines containing granite rocks on which emerged acidic soils, mostly Podzols (Piotrowska *et al.* 2015, Skiba *et al.* 2015). In each sample plot we recorded and measured all of the trees over 7 cm of diameter at breast height (dbh). Furthermore, we counted 90 specimens of young trees and shrubs closest to the centre of the plot but not exceeding a radius of 12.62 m (Bodziarczyk *et al.* 2019, Szwagrzyk *et al.* 2020).

The systematic sampling grid is limited only to the Polish Tatra Mts. and represents only silicate Swiss stone pine forests. Therefore, in order to compare the structure and composition of stand and shrub layer between silicate and calcicolous *P. cembra* forests we used another approach of data collection. We made 108 relevés based on the Braun-Blanquet method (Braun-Blanquet 1964, Dzwonko 2008) in the entire range of distribution of *P. cembra* forests in the Tatra Mts. (917 ha) (Zięba *et al.* 2018, 2019) from which we obtained the cover of tree and shrub species. We also measured the inclination (°) and altitude (m a.s.l.) of the centre of relevé. The area of the majority of the relevés had a size of 250 m^2. For the further analysis we chose only those representing silicate *Vaccinio-Pinetum cembrae* (77 relevés) and calcicolous *Swertio perennis-Pinetum cembrae* (14 relevés) (Fig. 1) (Zięba *et al.* 2018).

Data analysis

Based on the data from the circular sampling plots we estimated the stand composition of *P. cembra* forests according to number of trees per ha and BA per ha. Furthermore, we grouped all of the trees into 10 cm dbh classes and determined the general stand dbh structure as well as the dbh structure of each species.

Similar calculations were done for the *P. abies* forests which allowed for comparison of the structure of these two types of forests. We compared the BA per ha in the Swiss stone pine forests and Norway spruce forests as well as the BA per ha of *P. cembra* and *P. abies* in the Swiss stone pine forests using the *t*-test. Due to the lack of homoscedasticity, we used the Mann-Whitney U test for the comparison of the density of the trees (number of trees per ha) in the Swiss stone pine forests and Norway spruce forests. For checking the normality of distribution of variables we used the Shapiro-Wilk test, whereas the homoscedasticity was checked by using the Levene's test and Brown-Forsythe test (Quinn and Keough 2002, Fox and Weisberg 2019).

In addition to this, we compared the dbh distribution between the Swiss stone pine forests and Norway spruce forests, as well as the dbh distribution of *P. abies* in these two types of forests. We also checked the differences in the dbh distribution of *P. cembra* and *P. abies* in the *Vaccinio-Pinetum cembrae*. For all these analyses we used the Kolmogorov-Smirnov test (Quinn and Keough 2002).

Furthermore, we analysed the structure of young trees (< 7 cm dbh) and shrubs in the Swiss stone pine forests and in the Norway spruce forests based on the number of individuals per ha. We checked the differences in the density of young trees in the *Vaccinio-Pinetum cembrae* and *Plagiothecio-Piceetum* using the Mann-Whitney U test. We also compared the density of the two species most abundant among young trees: *S. aucuparia* (Mann-Whitney U test) and *P. abies* (*t*-test) in both types of forests. The normality and homoscedasticity were checked by using the same procedures as in the case of stand analysis.

Based on the data from the 91 relevés we compared the structure of tree and shrub layer between the silicate (*Vaccinio-Pinetum cembrae*) and calcicolous (*Swertio perennis-Pinetum cembrae*) Swiss stone pine forests. Prior the analysis we changed the species covers from the classic Braun-Blanquet scale into percentage scale (van der Maarel 1979, Dzwonko 2008). We compared the cover of main tree species occurring in these forests: *P. cembra*, *P. abies*, *L. decidua*, *S. aucuparia* and Carpathian downy birch (*Betula pubescens* ssp. *carpatica*) and main species representing the shrub layer: dwarf pine (*Pinus mugo*), Silesian willow (*Salix silesiaca*), *B. pubescens* ssp. *carpatica*, *P. cembra*, *P. abies* and *S. aucuparia* (Zięba *et al.* 2018). We used the Mann-Whitney U test for these comparisons. We took $P < 0.05$ significance level in case of all of the statistical tests.

To investigate the changes in the share of two main tree components of the Swiss stone pine forests, *P. cembra* and *P. abies* along the altitude (m a.s.l.) and inclination (°) gradients we used the generalized additive model (GAM) (Wood 2017). For these analyses we used the data from the entire range of distribution of Swiss stone pine forests in the Tatra Mts. which had measured the altitude and inclination (83 relevés from both *Vaccinio-Pinetum cembrae* and *Swertio perennis-Pinetum cembrae*). We did not include in the dataset one relevé with unusually low altitude (1039 m a.s.l.) which was located in a very small patch of *Swertio perennis-Pinetum cembrae* in the Belianske Tatra Mts. We fitted the models using the Restricted Maximum Likelihood (REML) method (Wood 2011, 2017).

All analyses were done in the statistical software, R version 3.6.1 (R Development Core Team 2019) using the 'car' (Fox and Weisberg 2019), 'nortest' (Gross and Ligges 2015), stats (R Core Team 2019) and mgcv (gam and gam.check functions) (Wood 2011, 2017) packages.

RESULTS

The mean density of trees in *P. cembra* forests reaches 618 stems/ha (standard deviation (SD) ± 326). The most numerous tree in the Swiss stone pine forests is *P. abies* (mean: 420 trees/ha, SD ± 258) which amounts 68% of the share of stand. *P. cembra* (mean: 148 trees/ha, SD ± 120) makes 24%. The rest are *S. aucuparia* (6%) and *B. pubescens* ssp. *carpatica* (2%) (Table 1).

Species composition of the stand based on the BA/ha is different (Table 1). The mean BA/ha is 23.17 m^2/ha (SD ± 15.6). In this case *P. cembra* is the dominant species (mean: 11.86 m^2/ha, SD ± 8.8) ÷ 51%, while *P. abies* (mean: 10.69 m^2/ha, SD ± 9.7) has a share of 46% in the stand. However, this difference is statistically insignificant (*P*-value = 0.8037). The admixture species amount only to 3%.

As shown in Fig. 2. *P. abies* dominates in the lower thickness classes (7÷29 cm), whereas *P. cembra* grows to large sizes (30÷69 cm) which only few spruces may reach and none of the broadleaved admixture species. The differences in dbh distribution between *P. abies* and *P. cembra* are significant (*P*-value < 0.05).

The species composition of typical Norway spruce forests differs considerably in comparison to Swiss stone pine forests (Table 1). The stand is dominated (99%) by *P. abies*. The list of admixture species varies from those in *Vaccinio-Pinetum cembrae*. Except for *B. pubescens* ssp. *carpatica* and *S. aucuparia* also goat willow (*Salix caprea*) sporadically occurs. None *P. cembra* trees were recorded.

The mean density of the trees in the Norway spruce forests is higher than in the Swiss stone pine forests and reaches 1123 trees per ha (SD ± 638). However, this difference is insignificant (*P*-value = 0.09265).

Table 1. Comparison of tree, regeneration (juveniles) and shrub layers structure between Swiss stone pine forests (*Vaccinio-Pinetum cembrae*) and upper montane Norway spruce forests (*Plagiothecio-Piceetum*) in the Tatra Mts.

Species	*Vaccinio-Pinetum cembrae*			*Plagiothecio-Piceetum*		
	trees (ha^{-1})	BA (m^2 ha^{-1})	ind. (ha^{-1})*	trees (ha^{-1})	BA (m^2 ha^{-1})	ind. (ha^{-1})*
Pinus cembra	148	11.86	60	0	0.00	0
Picea abies	420	10.69	525	1110	41.09	385
Sorbus aucuparia	38	0.34	325	5	0.13	50
Betula pubescens ssp. *carpatica*	12	0.28	33	3	0.02	0
Salix silesiaca	0	0.00	15	0	0.00	0
Salix caprea	0	0.00	0	5	0.14	0
Salix aurita	-	-	0	-	-	3
Pinus mugo	-	-	32	-	-	0
Lonicera nigra	-	-	0	-	-	25

*number of juvenile trees or shrubs (individuals); BA - basal area

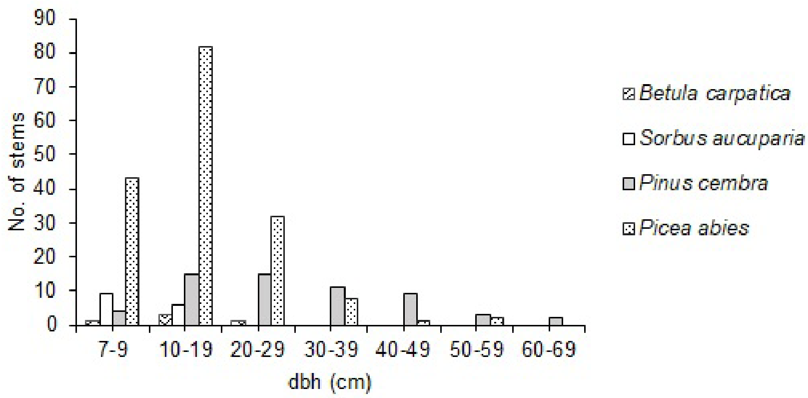

Fig. 2. The diameter at breast height (dbh) distribution of Swiss stone pine forests in the Tatra Mts. collected in eight permanent sampling plots in the Białka Valley.

The mean BA/ha in the *Plagiothecio-Piceetum* amounts 41.39 m^2/ha (SD ± 16.6) which is significantly higher (*P*-value < 0.05) than in *Vaccinio-Pinetum cembrae*.

The dbh distribution varies significantly (*P*-value < 0.05) in these two types of forests. The thickness structure of *P. abies* forests is characterized by higher number of trees in the lower classes than in the *P. cembra* forests. However, the thickest trees (over 50 cm in dbh) occurred almost only in the *Vaccinio-Pinetum cembrae* (Fig. 3) and they were indeed Swiss stone pines. Likewise the dbh distribution of *P. abies* differs significantly (*P*-value < 0.05) between Norway spruce and Swiss stone pine forests.

The dominant species in the shrub layer were *P. abies* (53%) (mean: 525 individuals/ha, SD ± 404) and *S. aucuparia* (33%) (mean: 325 individuals/ha, SD ± 382). Young individuals of *P. cembra* represented only 6% (mean: 60 individuals/ha, SD ± 50) of tree regeneration which differed significantly in comparison to Norway spruce (*P*-value < 0.05). The rest of the shrub layer consisted of typical shrubs (*P. mugo* – 3%, *S. silesiaca* – 2%) or pioneer trees such as *B. pubescens* ssp. *carpatica* (3%) (Table 1).

In the *Plagiothecio-Piceetum* a shrub layer consists only of two species (*P. abies* – 83%, *S. aucuparia* – 11%) that may built the next generation of stand. They dominate over two other species of shrubs that occur in these forests (Table 1). Interestingly, the tree regeneration of Norway spruce (mean: 395 individuals/ha, SD ± 362) does not vary significantly between *P. abies* and *P. cembra* forests (*P*-value = 0.5091). In case of *S. aucuparia* (mean: 53

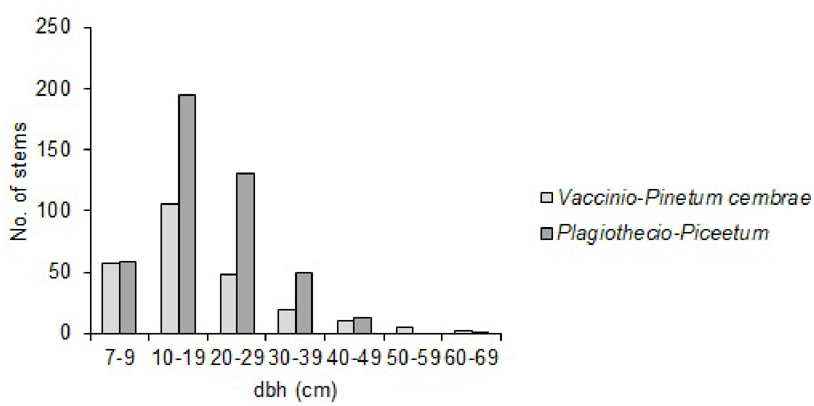

Fig. 3. Comparison of diameter at breast height (dbh) distribution of Norway spruce forests (*Plagiothecio-Piceetum*) and Swiss stone pine (*Vaccinio-Pinetum cembrae*) forests in eight plots per each community in the Białka Valley.

individuals/ha, SD ± 63), a young generation is significantly less numerous in the *Plagiothecio-Piceetum* than in *Vaccinio-Pinetum cembrae* (*P*-value < 0.05).

The species composition as well as the cover of main tree species in silicate and calcicolous Swiss stone pine forests in majority do not differ significantly. In both cases *P. cembra* and *P. abies* are the main tree species, whereas the other species form admixtures with relatively low cover. The only significant difference is almost complete lack of *L. decidua* in *Swertio perennis-Pinetum cembrae* (Table 2).

Likewise the species composition and cover of species in the shrub layer of both types of forest are similar. Three most common species are *P. mugo*, *P. abies* and *S. aucuparia*. The only significant differences are: higher share of *P. mugo* in *Vaccinio-Pinetum cembrae*, higher share of *S. silesiaca* in *Swertio perennis-Pinetum cembrae* and lack of *L. decidua* in *Swertio perennis-Pinetum cembrae* (Table 2).

Altitude has a significant impact on the share of *P. cembra* (*P* < 0.01) and *P. abies* (*P* < 0.001) in the Swiss stone pine forests (Fig. 4 A, B). The cover of *P. cembra* increases with altitude (Fig. 4A). In case of *P. abies* we observe constant decline of cover of Norway spruce in Swiss stone pine forests along the altitudinal gradient (Fig. 4 B). *P. cembra* dominates in the forest patches located in higher elevations.

Inclination has only significant impact (*P* < 0.05) on the share of *P. cembra*. The mean cover of these trees growths approximately linear (edf = 1) from 25% in flat terrain to 50% on very steep (70°) cliff forests (Fig. 4C). In case of *P. abies* we observed the decline of the share of this species in the stand along the inclination gradient, however, this relationship was insignificant (*P* = 0.641; Fig. 4D).

Table 2. Comparison of species composition of tree and shrub (including juvenile trees) layers between silicate (*Vaccinio-Pinetum cembrae*) and calcicolous (*Swertio perennis-Pinetum cembrae*) Swiss stone pine forests (significance level: *P* < 0.05; n.s. – not significant; n/a – not applicable).

Species	*Vaccinio-Pinetum cembrae*		*Swertio perennis-Pinetum cembrae*		Results of the Mann-Whitney U test
	mean cover (%)	standard deviation	mean cover (%)	standard deviation	*P*-value
Tree layer					
Pinus cembra	39.2	24.8	34.3	29.6	n.s.
Picea abies	32.3	26.9	26.6	24.5	n.s.
Larix decidua	3.6	8.1	0.0	0.0	< 0.05
Sorbus aucuparia	0.5	1.3	3.8	7.5	n.s.
Betula pubescens ssp. *carpatica*	1.4	6.1	0.0	0.0	n.s.
Shrub layer					
Pinus mugo	24.9	23.6	10.4	18.5	< 0.05
Salix silesiaca	0.6	2.4	2.0	4.8	< 0.05
Betula pubescens ssp. *carpatica*	1.0	3.5	0.4	1.3	n.s.
Pinus cembra	1.8	4.1	0.4	1.3	n.s.
Picea abies	7.0	7.3	11.6	10.6	n.s.
Larix decidua	0.2	0.8	none	none	n/a
Sorbus aucuparia	4.6	6.0	2.4	4.8	n.s.

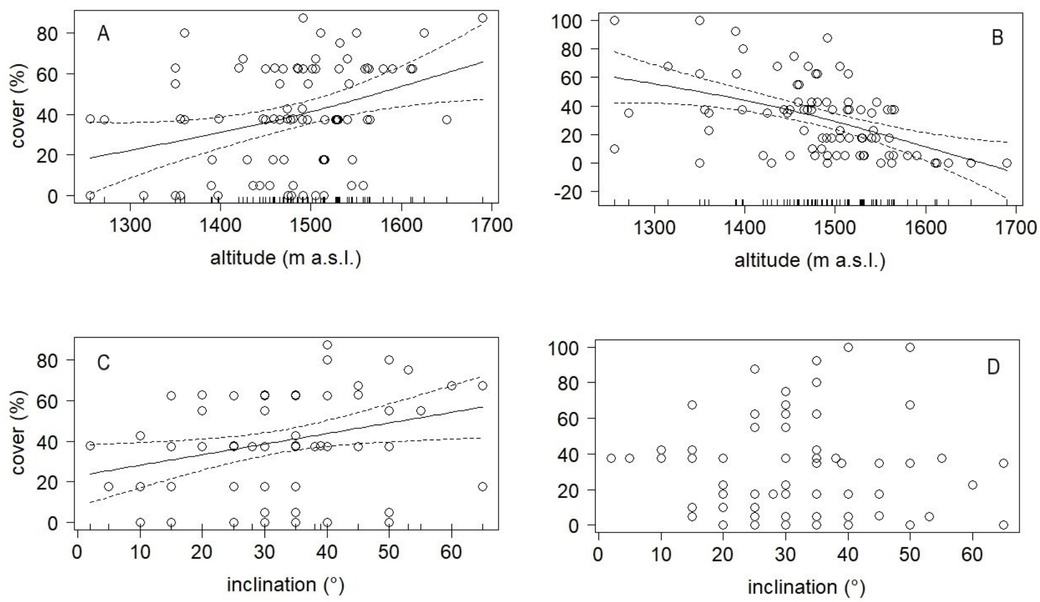

Fig. 4. Generalized additive model (GAM) models of the impact of altitude (m a.s.l.) and inclination (°) on the cover of *P. cembra* (A, C) and *P. abies* (B, D) in the tree layer of Swiss stone pine forests in the Tatra Mts. Dashed lines show the standard errors of a partial effect term combined with the standard errors of the model intercept.

DISCUSSION AND CONCLUSIONS

The tree density in Swiss stone pine forests in the Tatra Mts. is lower than in all forests of the Polish TNP (670 stems/ha) and considerably higher than the mean for the forests located at the elevation above 1400 m a.s.l. (462 stems/ha) (Bodziarczyk *et al.* 2019). Such a relatively low density in the high elevation forests might be related to the large bark beetle outbreaks in spruce-dominated stands in the TNP. In the *P. cembra* forests tree mortality is substantially lower (Bodziarczyk *et al.* 2019, Grodzki *et al.* 2019). The tree density recorded in the Swiss stone pine forests of the TNP matches the density measured in the subalpine stands of Polish High Tatra Mts. (Holeksa *et al*. 2006) and in Slovakian Tatra Mts. (Nefcerka Valley, Krizne) (Korpel 1989, Voško 1995). The average density of trees is lower than the density recorded by Vološčuk (2012) in a 0.5 ha sample plot located in the *P. cembra* stand at the southern side of the Tatra Mts. (836 stems/ha). In the Eastern Carpathians a broad range of tree density (311÷1155 stems/ha) of *P. cembra* forests along the altitude gradient (1450–1750 m a.s.l.) was found (Popa *et al.* 2017). Recent data from the Alps showed the densities of 281–593 stems/ha (Risch *et al.* 2003, Motta and Lingua 2005, Ballmer *et al.* 2014, Giammarchi *et al.* 2017). The most similar in terms of number of stems/ha to the forests from the Tatra Mts. are those from the Eastern Italian Alps (1860 m a.s.l.) (Giammarchi *et al.* 2017).

The density of *P. cembra* in the typical Swiss stone pine forests seems not to vary between northern and southern side of the Tatra Mts. Similar values were also recorded in the Eastern Carpathians (102÷149 stems/ha) (Popa *et al.* 2017). However, in Swiss stone pine forests in the Alps the density of *P. cembra* reaches higher values (179–481 stems/ha) (Risch *et al.* 2003, Motta and Lingua 2005, Giammarchi *et al.* 2017) than in the Carpathians.

Basal area (BA/ha) of *P. cembra* forests from the northern side of the Tatra Mts. is similar to those in the higher elevations (1750 m a.sl.) of Eastern Carpathians (*P. cembra* – 13.54 m^2/ha, total – 20.55 m^2/ha) (Popa *et al.* 2017) and in the Western Alps in Aletschwald (1660–2200 m a.s.l.) (total – 22.2 m^2/ha) and Cottian Alps (2010 m a.s.l.) (*P. cembra* ÷ 14.70 m^2/ha, total – 28.20 m^2/ha) (Mottta and Lin-

Table 3. Comparison of species composition of Swiss stone pine forests in Europe (based on basal area; m² per ha).

Location	Tatra Mts. (Białka Valley)	Tatra Mts. (Furkotská Valley)	Eastern Carpathians (Calimani Mts.)	Eastern Carpathians (Calimani Mts.)	Eastern Carpathians (Calimani Mts.)	Western Alps (Lago Perso)	Eastern Alps (Alta Val di Stava)
Altitude (m a.s.l.)	1233-1530	1520-1540	1750	1550	1450	2010	1860
Study area (ha)	0.4 (8 plots – 0,05 ha)	0.5 (1 plot)	2.1 (1 plot)	1.0 (1 plot)	0.5 (1 plot)	1.0 (1 plot)	1.0 (1 plot)
Source / Species	ms	1	2	2	2	3	4
P. cembra	11.86	18.90	13.54	13.80	16.28	14.70	31.50
P. abies	10.69	28.74	6.81	26.82	33.33	0.00	1.60
L. decidua	0.00	4.86	0.00	0.00	0.00	13.50	3.22
S. aucuparia	0.34	0.00	0.20	0.12	0.50	0.00	0.23

ms – this manuscript; 1 – Vološčuk 2012; 2 – Popa *et al.* 2017; 3 – Motta and Lingua 2005; 4 – Giammarchi *et al.* 2017

gua 2005, Ballmer *et al.* 2014). Greater BA/ha was also recorded at lower elevations in the Carpathians (Popa *et al.* 2017) and in southern Alps (*ca* 35–50 m²/ha) (Giammarchi *et al.* 2017) (Table 3).

Differences between *P. cembra* stands in the Carpathians and in the Alps are especially visible in the species composition (Table 3). In the Carpathians this type of subalpine forests is dominated by *P. abies* and *P. cembra*, whereas in the Alps by *P. cembra* and *L. decidua*. The presence of European larch is noticeable only in the southern slopes of the Tatra Mts. (Voško 1995, Vološčuk 2012, Zięba *et al.* 2018). However, even the relatively low share of *L. decidua* in the Carpathian *P. cembra* forests it is worth to emphasize that these subalpine phytocoenosis are one of the most important natural refugium of this species in this mountain range (Holeksa and Szwagrzyk 2004, Kempf *et al.* 2018, Zięba *et al.* 2018).

It is worth to add, that both in the Tatra Mts. and Eastern Carpathians, the stand composition differs considerably depending on the method of calculation (no. stems/ha *vs* BA/ha). *P. abies* is more numerous, whereas *P. cembra* reaches larger size (Popa *et al.* 2017). In the Alps *P. cembra* dominates over *L. decidua* both in abundance and size (Ballmer *et al.* 2014, Giammarchi *et al.* 2017).

Likewise in the Polish TNP, on the southern side of the Tatra Mts. *P. abies* (60.3%) and *S. aucuparia* (36.9%) also dominates among the juvenile trees over *P. cembra* (3.2%) (Korpel 1989). Even though the proportion of young trees seems to be unfavourable for Swiss stone pine it is worth to mention that long-term studies reveal significant increase in the regeneration of *P. cembra* in the Tatra Mts. (Zwijacz-Kozica and Żywiec 2007). In the Alps *P. cembra* is the most abundant young tree (60÷92%) followed by *L. decidua* and *S. aucuapria* (Mottta and Lingua 2005, Giammarchi *et al.* 2017). *Pinus montana* s. l. (= *P. mugo, P. uncinata*) seems to be the most common shrub, especially at the higher elevations in these forests across the Carpathians and Alps (Risch *et al.* 2003, Motta and Lingua 2005, Popa *et al.* 2017).

The differences between species composition of stand and shrub layer of silicate (*Vaccinio-Pinetum cembrae*) and calcicolous (*Swertio perennis-Pinetum cembrae*) are relatively low. It is probably linked to the species characteristics. Most of these trees and shrubs can grow both on acidic and calcareous soils (Zarzycki *et al.* 2002). Silicate and calcicolous *P. cembra* forests vary predominantly in the ground flora composition (Zięba *et al.* 2018).

The most visible difference in species composition between Swiss stone pine forests in the Tatra Mts. and in the Alps is the higher share of *L. decidua* in all layers and both on silicate and calcareous bedrock in the Alps. *P. mugo* unlike in the Tatra Mts. is more common in the calcicolous Swiss stone pine forests than on granitic (Willner and Grabherr 2007). Furthermore, in the calcicolous Swiss stone pine forests in the Alps (*Rhododendro hirsuti-Pinetum cembrae*) false medlar (*Sorbus chamaemespilus*) occurs frequently (Willner and Grabherr 2007), whereas in the Tatra Mts. it is only sporadic (Zięba *et al.* 2018). In addition to this, in the Alps *S. silesiaca* is replaced by alike *Salix appendiculata*. Another shrub which does not occur in the Tatra Mts. and is common in the alpine Swiss stone pine forests is green alder (*Alnus alnobetula*) (Willner and Grabherr 2007).

The increase of the share of *P. cembra* and decrease of *P. abies* along the altitude gradient seems to be apparent. Similar tendency was recorded both in the Carpathians and in the Alps (Caudullo and de Rigo 2016, Giammarchi *et al.* 2017, Popa *et al.* 2017).

Inclination has a significant impact on the occurrence of Swiss stone pine forests in the Tatra Mts. The probability of their occurrence increases along the gradient of inclination. Majority of these forests in the Tatra Mts. occur on steep (20÷50°) and rocky slopes (Zięba *et al.* 2019). Steep slopes seem to support the growth of *P. cembra*. That can be probably explained by the lower intensity of competition for light on the steep slopes as tree crowns are more separated than on a flat terrain. However, we did not find evidence of significant decrease of *P. abies* along the inclination gradient as it was assumed before (Holeksa and Szwagrzyk 2004, Zięba *et al.* 2019).

The recent research on the genetic diversity, insect and fungus diseases, as well as the structure and distribution in the Tatra Mts., seems to confirm appropriate state of conservation of *P. cembra* forests in the Tatra Mts. (Zwijacz-Kozica and Żywiec 2007, Dzialuk *et al.* 2014, Pusz *et al.* 2018, Grodzki *et al.* 2019, Zięba *et al.* 2019). However, the current climatic trends may bring a threat to these forests (Casalegno *et al.* 2010). Therefore, it seems to be advisable to know their dynamics in the Tatra Mts. based on the provided structural data. So far studies regarding mixed stands of Norway spruce and European larch from the southern Tatra Mts. have revealed a high dependence of natural regeneration of these forests to large-scale disturbances (Zielonka *et al.* 2010). Likewise Swiss stone pine forests from the Eastern Carpathians seem to be shaped by large-scale disturbances, whereas small disturbances may lead to support the regeneration of *P. abies* and slow displace of *P. cembra* from the stand (Popa *et al.* 2017).

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