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The aims of this study were to describe the biometrics and the spatial and age structure of a population of Norway spruce, to compare vertically connected sections of the timberline ecotone, and to assess the possibility of regeneration of a Norway spruce population under the conditions of the ecotone developing above the former pastoral timberline in the Hrubý Jeseník Mountains, Czech Republic. In the first stage, we established the age of the populations by means of an age–girth nonlinear regression model in a research polygon (RP) with an area of 3.5 ha. The degree of coverage was determined by using geographic information system methods. The total number of cones in the RP was counted, and 50 cones were taken for laboratory investigation of their germination capacity and the number of seeds per cone. The distribution of trees in clonal generations was examined for 10 clonal groups, and the characteristics of layering were explored by measuring the preserved layered branches. To verify the trends found in the first stage of research, we conducted an analysis of the age of all specimens on 8 control plots (50 m × 30 m) in other parts of the mountain range. The results show that the timberline ecotone is rising gradually and that the forest-free area may become significantly reduced. Up to 3 generations of trees of clonal origin were found in the RP. A greater intensity of vegetative regeneration was observed in the upper section of the RP. Moreover, the seed-based regeneration proved to be successful in the RP, and living, germinating seeds were found even in the top parts of the RP.

Keywords: Norway spruce; alpine timberline; population structure; seed-based regeneration; clonal groups; timberline dynamics; Czech Republic.

Introduction

The alpine timberline ecotone (ATLE) is one of the most significant biogeographic borders in a mountain landscape (Troll 1973; Becker et al 2007; Holtmeier 2009). Because of the response of vegetation to climate change, the ATLE is considered to be a sensitive indicator of this phenomenon (Baker et al 1995; Kimball and Weihrauch 2000). The only globally determining factor of timberline is temperature conditions (Körner 1999; Körner and Paulsen 2004). However, the position of the timberline and the structure of the woody plant population are affected by several other factors (Plesník 1971; Arno and Hammerly 1984; Treml 2007; Holtmeier 2009), among which the following are important: intense wind pressure (Holtmeier and Brol 2010), local irregularities in the distribution of snow cover (Mellman-Brown 2005), avalanche activity, and relief factors (Treml and Banaš 2000). Frequently, these factors interact, for example, the properties of relief, wind intensity, and direction affect the relocation of snow (Holtmeier 2005). A

key factor that has influenced the physiognomy of the timberline ecotone in the mountain ranges of central Europe is anthropogenic activities (Plesník 1971; Treml and Banaš 2000; Treml 2007; Sarmiento and Frolich 2002; Sitko and Troll 2008; Holtmeier 2009). In the European Alps, the Carpathian Mountains and many other high mountains of Eurasia, and in most tropical high mountains, almost no untouched mountain forests remain. The type and intensity of human impact on timberlines also are different. However, a depression of 150 to 300 m below the uppermost postglacial level of the climatic timberline can be accepted as an average value (Holtmeier 1974). The timberline ecotone in the Hrubý Jeseník Mountains has been considerably affected by grazing and the related burning of trees, and by haymaking and logging (Hošek 1973; Jeník and Hampel 1992). Therefore, the current timberline in the Hrubý Jeseník Mountains can be referred to as the former pastoral timberline (Kozak et al 1995), and it is characterized by a narrow width of the ecotone (the "kampf" zone) (Treml and Banaš 2000).

With regard to tree species composition, the current ATLE is naturally formed exclusively by Norway spruce (*Picea abies*), without the natural presence of dwarf pine; this species was introduced in the area during afforestation in the late 19th and early 20th centuries (Treml and Banaš 2000). In the context of the natural central European range of spruce, the situation in the Hrubý Jeseník Mountains is unique (Maděra 2004; Král 2009) because, in other mountain ranges, the stands of spruce on the alpine timberline (ATL) are accompanied by other woody plant species that reach even higher (*Pinus cembra*, *Pinus mugo*, *Larix decidua*, *Rhododendron* spp, *Alnus viridis*). Therefore, spruce may occupy the space of the dwarf pine, which receded during the development of vegetation in the Holocene (Rybníček and Rybníčková 2004). Whether this is a natural timberline (Jeník 1961; Treml and Banaš 2000; Jeník and Štursa 2003) or a timberline artificially conditioned by human activity (Hošek 1973; Novák et al 2010), it is highly interesting to monitor the behavior of spruce at the limit of its ecological valence. The reduced ability of the Norway spruce to propagate generatively is replaced by vegetative regeneration, when a clonal tree (layer) is formed by the rooting (layering) of a plagiotropic branch (after rooting, the branch is referred to as a layering branch) of the initial parent tree (Kuoch and Amiet 1970; Traquillini 1979; Holtmeier 2009). The aims of the present study were (1) to describe the biometrics and age structure of the populations, (2) to compare 2 vertically connected sections of the timberline ecotone, and (3) to assess the possibility of regeneration of the Norway spruce population under the conditions of the ecotone developing above the former pastoral timberline in the Hrubý Jeseník Mountains.

Material and methods

Study area
The highest elevation of both the Hrubý Jeseník Mountains, the approximate center of the study area is at 50°04′N and 17°14′E (Figure 1), and the Giant Mountains, in fact, are the only islands of natural alpine forest-free areas between the Scandes to the north and the Alps and West Carpathians to the south (Jeník and Štursa 2003). In the Hrubý Jeseník Mountains, there are 7 elevations at which the ATL has been defined (Treml and Banaš 2000); the upper line of 2-m tall spruce trees has only been defined in the areas of Keprník, Vysoká Hole, and Praděd (Treml 2007). The average altitude of the ATL (minimal canopy, 50%; minimal height of trees, 5 m; and minimal area, 100 m^2) in the Hrubý Jeseník Mountains is 1301 m (Treml and Banaš 2000). The highest parts of Keprník (1423 m), Vysoká hole (1463 m), and Praděd (1492 m) are the only locations in the Hrubý Jeseník Mountains, where there are unique patterned ground (Treml and Křížek 2006) and wind-blown alpine grassland (Chytrý et al 2001)

made up of an alliance of *Juncion triffidi* (as *Carici rigidae–Juncetum trifidi*, Šmarda 1950 and *Cetrario–Festucetum supinae*, Jeník 1961) with arcto-alpine species (*Carex bigelowii*, *Juncus trifidus*, *Diphasiastrum alpinum*, *Hieracium alpinum*, and abundant lichens and mosses, including *Cetraria* spp and *Cladonia* spp).

Research polygon and control plots
The first, more detailed, stages of field data collection were conducted in the research polygon (RP) located in the area of the summit of Keprník in 2009. The RP was bordered by a hiking trail on the east and a vegetation line of an artificially planted closed stand of the dwarf pine on the west. The RP was divided into 2 sections in the altitudinal direction (Figure 1). The lower section (lower RP) was limited by the upper line of 5-m-tall spruce trees (with an average altitude of 1382 m) and the upper line of 2-m-tall spruce trees (with an average altitude of 1407 m); these lines were identified by Treml (2007) in the 2005 growing season. The upper section (upper RP) was defined by the upper line of 2-m tall spruce trees (1407 m) (Treml 2007) and the summit of Keprník (1423 m). The areas and inclinations of the lower and upper sections are 20,380 m^2 (18%) and 15,258 m^2 (11%), respectively. The RP is exposed to the northwest.

To verify whether the trends found in 2009 can be found in other parts of the mountain range, 4 control plots (CPs) in the area of Praděd and 4 CPs in the area of Vysoká hole were established in the second stage of field data collection (Figure 1). The CPs were located in complementary expositions, that is, 2 plots were located with one approximately above the other in each exposition: one of them in the area of the upper line of 5-m-tall spruce trees (Treml 2007) and one in the area of the upper line of 2-m-tall spruce trees (Treml 2007). The size of the CP was 50 m (contour line) × 30 m (line perpendicular to the contour).

Field data collection
The fieldwork in the RP was carried out in 2009. All living and dead specimens of the Norway spruce 10 cm tall or taller were measured (shorter specimens were not recorded because of the thick grass–herb vegetation). For the living specimens, the girth at the stem base (by using a tape with 1-cm accuracy) and the height (by using a height-measuring staff with 5-cm accuracy) were measured. For dead specimens (including stems on the ground), only the girth at the stem base was measured. All seedlings up to a height of 80 cm that had not layered were recorded. A representative number (lower section, 94; upper section, 21) of randomly chosen specimens was sampled from the stem base by means of a Pressler borer. The age of specimens with a small stem diameter, where a core could not be acquired, was established by destructive methods.

FIGURE 1 Position of the Hrubý Jeseník Mountains in Europe (A); elevations in the Hrubý Jeseník Mountains where the alpine timberline was defined according to Treml and Banaš (2001), with the upper lines of 5-m-tall spruce trees and 2-m-tall spruce trees defined according to Treml (2007) (B); and aerial photos of the research polygon and control plots (C–E). (Map by the authors)
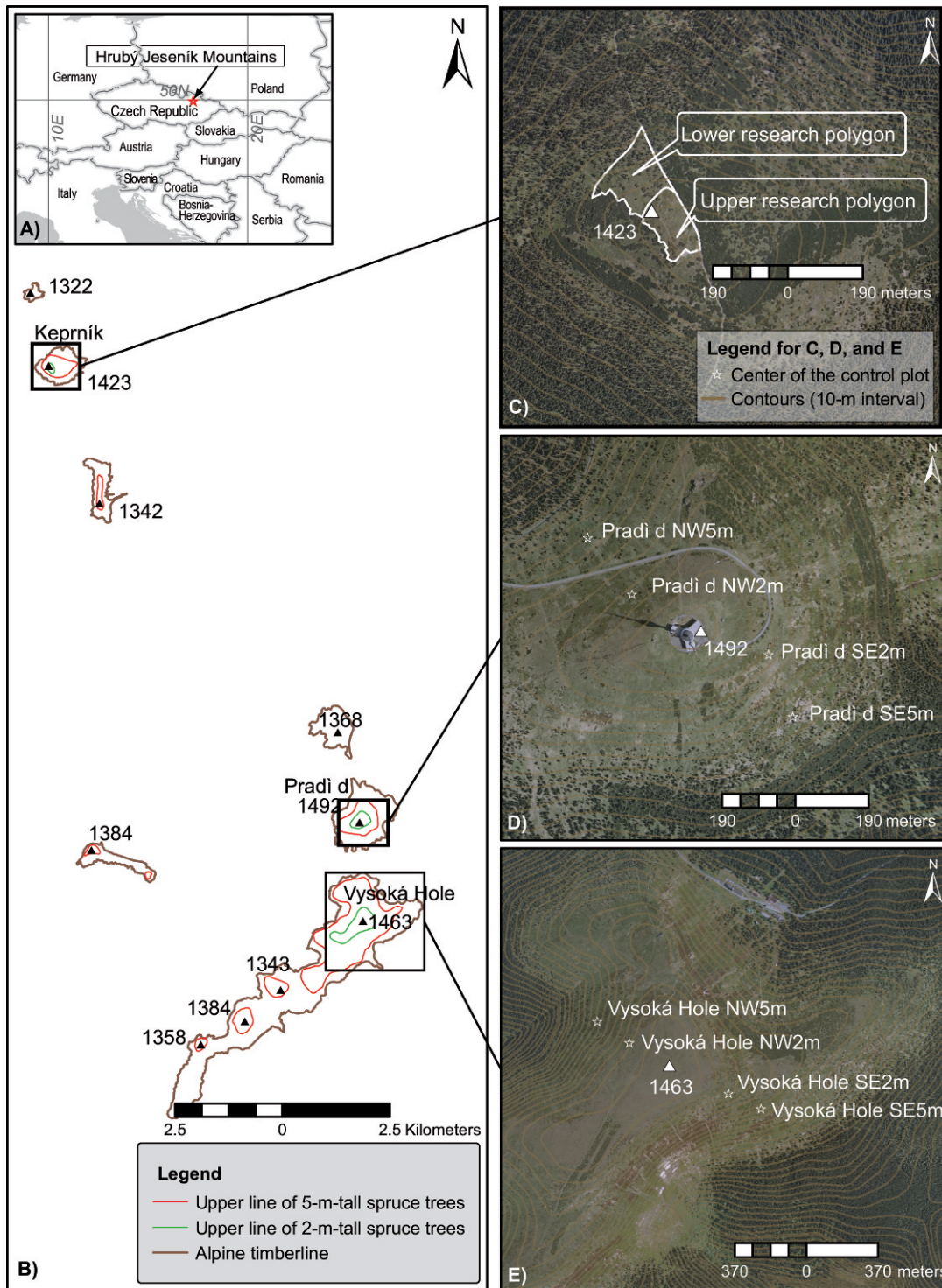
The clonal relationships were explored in detail in 10 randomly selected clonal groups (6 in the lower RP and 4 in the upper RP). We determined the numbers of living and dead trees of individual generations within a clonal group by uncovering the preserved layering branches. For layering branches, the height of their position in the parent tree, the distance, and the direction of rooting from the parent tree were measured. Individual generations were counted by starting from the oldest specimen, even if it was already dead.

All fertile specimens and the total number of their cones were recorded in 2008 and 2009. At the end of the vegetation period in 2008, 50 randomly chosen cones (25 pieces in each section of the RP) were taken with the purpose of assessing their basic characteristics (number of seeds in a cone, germination capacity).

In 2010, an age analysis was performed at 8 CPs (Figure 1). On each plot, all living specimens of spruce 10 cm tall or taller were bored at the stem base. The ages of specimens with small stem diameters were determined destructively. In addition, the number of seedlings was counted in all CPs.

Laboratory work

The surface of the samples was sanded, and the number of tree rings was counted by using a binocular microscope (LEICA S6D). The cones that had been collected in the field were broken open, and the total number of seeds in each cone was counted. We used randomly selected seeds (4 × 100 seeds for each RP section) to test their germination capacity (the number of germinated seeds during the entire period of the germination test, that is, 21 days, expressed as a percentage of the seeds) in compliance with valid norms (CNS 481211 /2006/).

Data analysis

By using the established age and stem girth, a nonlinear regression model was created: the Chapman-Richards growth function (Šmelko et al 1992; Zhang 1997). This was used for the calculation of the population age structure model in the RP. The Chapman-Richards growth function is expressed by the following formula:

$$y = A * \left[1 - e^{-b*x}\right]^{1/c} \tag{1}$$

where y is the girth at age x, b and c are parameters that have been determined by the "least square" method, and A is the asymptote that was established by fixing it as the value that corresponds to the tree on the site with the highest girth (Brewer et al 1985). The goodness of the fit (R^2) was calculated by the following equation (Sweda and Kouketsu 1984):

$$R^2 = 1 - \frac{\sum_{i=1}^{n} (Y_i - y_i)^2}{\sum_{y=1}^{n} (Y_i - \overline{Y})^2} \tag{2}$$

where R^2 is the coefficient of determination, Y_i is the observed value at age i, y_i is the calculated value at age i, $\overline{Y}$ is the average of the actual observation, n is the total age of the sample tree, and f is the number of parameters involved in the equation concerned.

To calculate the growth function and to conduct the data analyses, we used the tools of the STATISTICA 9 and Microsoft Excel 2003 programs. Statistical testing was carried out at a level of significance of α = 0.05. The degree of coverage was determined on the basis of the proportion of the area (the category of tree). The area of the category "tree" was determined by creating a vector layer that defined individual trees and clonal groups over a layer of orthogonal images (pixel 20 × 20 cm, taken in 2008) in the ArcGIS 9 program. The size of the CP was designed so that the age could be established in a direct way for all specimens: the age structure could thus be ascertained without the use of the growth function.

Results

Population structure in the RP

In total, 1389 living specimens and 220 dead specimens of spruce were recorded in the RP. In the lower section, there were 953 living specimens (467.6 specimens/ha) and 209 dead specimens (102.6 specimens/ha); in the upper section there were 436 living specimens (285.8 specimens/ha) and 13 dead specimens (8.5 specimens/ha). The degree of coverage of spruce in the lower RP was 10.8% (spruce area, 2198.4 m², and in the upper RP, it was 1.6% (spruce area, 238.7 m²).

In the lower RP, the most specimens were within the 201–400-cm height class; it is important that, even though the lower RP was above the upper line of 500-cm-tall spruce trees (Treml 2007), 27 specimens that exceeded that height were found here. In the upper RP, the most specimens were within the 81–200-cm height class. In total, 57 specimens exceeded a height of 200 cm, in spite of the fact that the upper RP is above the upper line of 200-cm-tall spruce trees (Treml 2007) (Table 1).

In both sections of the RP, the highest proportion of specimens were within the lowest girth class; the proportion decreases with increasing girth. The mortality in the lower section was the highest (31.2%) in the 61+ cm girth class, and the mortality in the upper section was the highest (3.8%) in the 31+ cm girth class. The total mortality in the upper RP was considerably lower (2.9%) than in the lower section (18.0%) (Table 2).

The regression between the stem girth and the age of the trees as established by the core was statistically significant. Thus, the age of trees was modeled by using the regression formula for the lower and upper sections of the RP (Figure 2A and B).

The growth function has the following form for the RP lower section:

$$y = 217 * \left[1 - e^{-0.003455*x}\right]^{1/0.960064} \tag{3}$$

The growth function has the following form for the RP upper section:

$$y = 62 * \left[1 - e^{-0.01249*x}\right]^{1/0.996429} \tag{4}$$

The highest proportion of trees (23.9%) in the lower section was within the 21–40-year age class. Toward

TABLE 1 Number of living trees ≥10 cm by height classes.

Height classes	Lower RP		Upper RP	
	n - trees	Proportion %	*n* - trees	Proportion %
10–80 cm	109	11.4	158	36.2
81–200 cm	230	24.2	221	50.7
201–400 cm	443	46.5	57	13.1
400–500 cm	144	15.1		
501 cm +	27	2.8		

higher ages, the proportion decreased to a value of 0.3%, which represents the oldest age class (181–200 years). In the upper section, the highest proportion of specimens was in the youngest age class (59.2%), and there was a gradual decrease in proportion toward older age classes (Figure 3).

Another insight into the age structure of the population is provided by the proportion of trees in the individual generations in clonal groups (Table 3). In the lower section, 11 initial parent trees had produced 49 first-generation layers: these had produced 23 second-generation layers, and the second-generation layers had given birth to 5 third-generation layers. In the upper section, one generation fewer was recorded. In total, 5 initial parent trees had produced 64 first-generation layers, and these had produced 10 second-generation layers. When considering the above-mentioned data with respect to the entire RP, one primary parent tree has 7.1 direct descendants, that is, first-generation layers. The first-generation layers only produced 0.3 second-generation layers on average, and the second-generation layers produced 0.2 third-generation layers (Table 3). The

speed of spruce propagation decelerates starting in the second generation in both sections of the RP. A statistically significant difference (Mann-Whitney *U*-test, $P < 10^{-5}$) in the number of first-generation layers produced by one parent tree was recorded between the lower (average value ± SE = 4.5 ± 1.06) and the upper (average value = 12.8 ± 4.18) sections of the RP.

Seed-based and vegetative regeneration in the RP

The potential of seed-based regeneration of spruce under these conditions is not high; however, it is important that it is still apparent. In the lower RP 1325 cones in total (650 cones/ha) were found. Cones were found in 9.9% of specimens. In the upper RP, 29 cones were found (19 cones/ha). Cones were found in 1.2% of all specimens. The average number of cones per fertile specimen in the lower section (14.1 ± 1.88) was higher than in the upper section (5.8 ± 1.32). There was a statistically significant difference (Student *t*-test, $P < 10^{-4}$) in the number of seeds per cone between the lower (average value, 70.2 ± 6.50) and the upper (average value, 42.2 ± 5.42) sections of the RP. The average value of the germination capacity in the lower

TABLE 2 Ratio of dead trees to living trees by girth classes.

Girth class	Total	%	*n* - living	%	*n* - dead	%
	Lower RP					
1–30 cm	535	46.0	496	92.7	39	7.3
31–60 cm	454	39.1	338	74.4	116	25.6
61+ cm	173	14.9	119	68.8	54	31.2
Sum	1162	100.0	953	82.0	209	18.0
	Upper RP					
1–15 cm	295	65.7	287	97.3	8	2.7
16–30 cm	128	28.5	124	96.9	4	3.1
31+ cm	26	5.8	25	96.2	1	3.8
Sum	449	100.0	436	97.1	13	2.9

FIGURE 2 Nonlinear regression (Ch-R growth function) between stem girth and tree age: (A) in the RP lower section, all parameters are statistically significant, $P < 10^{-7}$; parameter b interval estimate (0.002585–0.004326), parameter c interval estimate (0.822537–1.097591); $R^2 = 0.8044$, $n = 94$, asymptote fixed at 217; (B) in the RP upper section, all parameters are statistically significant, $P < 10^{-4}$, parameter b interval estimate (0.004908–0.020071), parameter c interval estimate (0.451770–1.541088); $R^2 = 0.7463$, $n = 21$, asymptote fixed at 62.
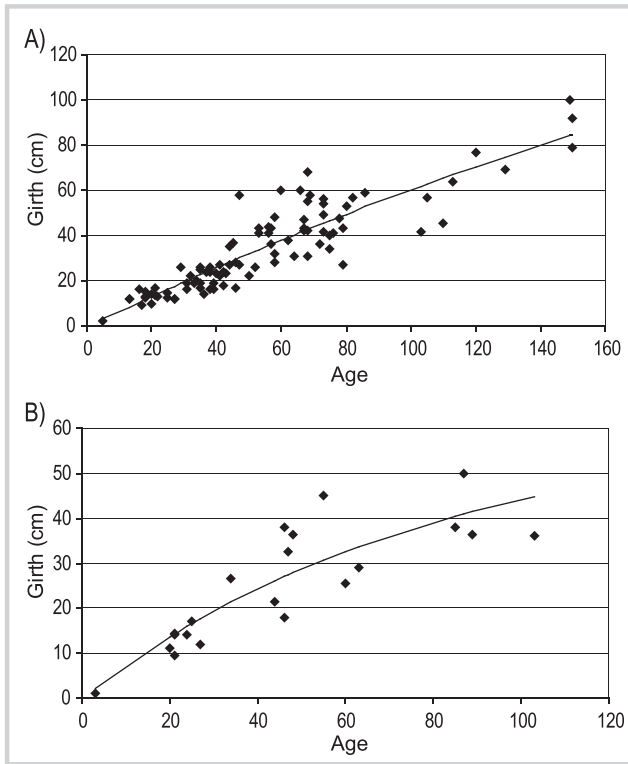
section (27.0 ± 3.67) was slightly higher than in the upper RP (20.5 ± 2.90), but the difference for the basic set was not statistically significant (Student t-test, $P = 0.21$). The estimated potential of the seed-based regeneration (estimation based on the number of cones, the average number of seeds per cone, and the average germination capacity) was 12,320 germinating seeds per hectare in the lower RP, and 164 germinating seeds per hectare in the upper RP (Table 4).

In total, 109 seedlings were recorded in the RP: 50 in the lower section (25 specimens per hectare) and 59 in the upper section (39 specimens/ha). The 10–20-cm height class included 5.1% and 2.0% of seedlings in the lower and upper RP, respectively; the 21–40-cm height class included 40.7% and 32.0% of seedlings in the lower and upper RP, respectively. The 41–60-cm height class was represented by 35.6% and 40% of seedlings in the lower and upper RP, respectively, and the 61–80 cm height class by 18.6% and 26.0% of seedlings in the lower and upper RP, respectively.

The population solves the essential problem of survival and propagation at sites with a high intensity of stress and biomass disturbance by vegetative regeneration. There was a statistically significant difference (Mann-Whitney U-test, $P < 10^{-5}$) between the layering (rooting) distance in the lower RP (an average value of 93.0 ± 4.64) and the upper RP (an average value of 43.9 ± 3.12). Also, the difference in the height of layering branch position in the parent tree between the lower (average value of 25.9 ± 2.79) and the upper (an average value of 7.8 ± 0.73) RP was statistically significant

FIGURE 3 Distribution of specimens in the age classes on the RP and on the CP.
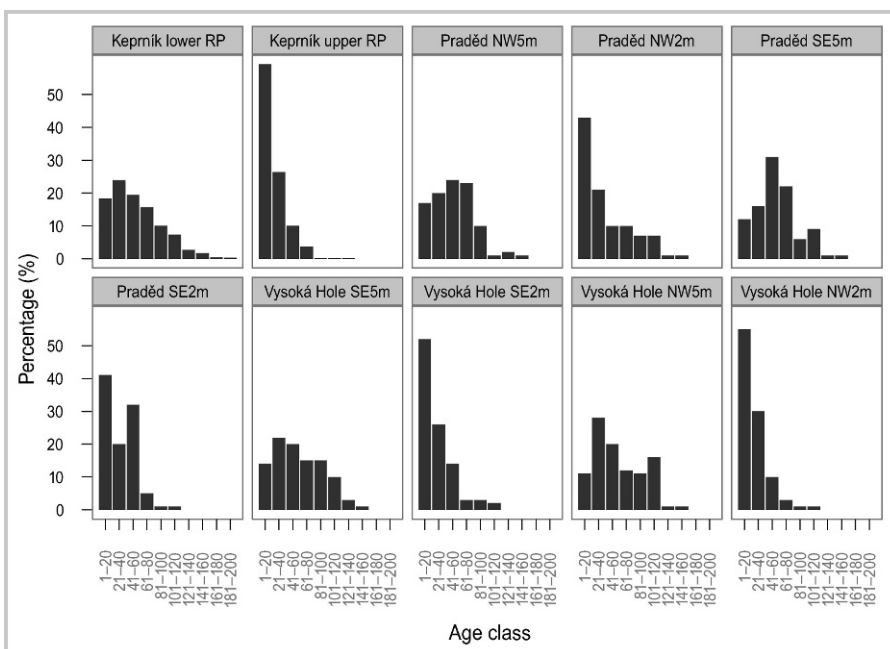
TABLE 3 Distribution of trees (l = living, d = dead) in individual generations in clonal groups, their number, and mortality (in relation to the total number of trees in clonal groups within a particular section of the RP).

Generation	Parent tree		1st generation		2nd generation		3rd generation		Not identified	
	Lower RP									
Living/dead	l	d	l	d	l	d	l	d	l	d
Number of trees	9	2	47	2	22	1	5	0	7	1
Proportion %	9.4	2.1	49.0	2.1	22.9	1.0	5.2	0.0	7.3	1.0
In total	11		49		23		5		8	
	Upper RP									
Living/dead	l	d	l	d	l	d	l	d	l	d
Number of trees	5	0	63	1	10	0				
Proportion %	6.3	0.0	79.7	1.3	12.7	0.0				
In total	5		64		10					

(Mann-Whitney U-test, $P < 10^{-4}$). Similar distribution of values and statistically significant differences (Mann-Whitney-U test, $P < 10^{-4}$) were observed when assessing these characteristics (the distance of layering, the height of layering branch position in the parent tree) in parent trees of similar age (Figure 4A–C). It was found that multiple trees can originate from one primary layering branch, because the branch can root at more than one spot. We found up to 5 clonal trees originating from one branch. The average number of trees from one primary branch was slightly higher in the upper RP (1.9 ± 0.18) than in the lower RP (1.6 ± 0.12), but a statistically significant difference was not found (Mann-Whitney U-test, $P = 0.22$). The same trend in the distribution of values was observed when this characteristic was assessed in parent trees of similar age (Figure 4).

In the lower section, layering occurred most often in the northwest (20%), southeast (20%), and southwest (18%) directions; in the upper section, layering was most frequent in the east (27%), northeast (19%), and north (19%) directions (Figure 5A and B).

Age structure of population on control plots

The distribution of specimens in age classes in the CPs in the lower part of the ecotone (Praděd NW5m; Praděd SE5m; Vysoká Hole NW5m; Vysoká Hole SE5m) was similar to that in Keprník. However, in the plots in Praděd, there was a higher proportion of specimens only of the third age class (not the second class), which is the main difference from the age structure at RP Keprník. Spruce populations in the lower part of the ecotone in all CPs were different from those of the RP because specimens in the 2 oldest age classes were absent (Figure 3).

The distribution of specimens in age classes in the CPs in the upper part of the ecotone (Praděd NW2m; Praděd

TABLE 4 Number of cones in the RP (per hectare), percentage of fertile specimens, average number of cones per fertile specimen, average number of seeds per cone, average germination capacity, and estimate of germinating seeds (vegetation period: 2008).

Fertility features	Research plot	
	Upper RP	Lower RP
Number of cones (n/ha)	19	650
Fertile specimens (%)	1.2	9.9
Cones per fertile specimen (average ± SE)	5.8 ± 1.32	14.1 ± 1.88
Seed per cone (average ± SE)	42.2 ± 5.42	70.2 ± 6.50
Seed germination capacity (%) (average ± SE)	20.5 ± 2.90	27.0 ± 3.67
Germinating seeds estimate (n/ha)	164	12,320

FIGURE 4 Distribution of values: (A) height of layering branch positions in the parent tree; (B) distance of layering from the parent tree; (C) number of trees originating from one primary layering branch. T = all parent trees; age classes of parent trees: 1 = 1–30 years, 2 = 31–60 years, 3 = 61–90 years.
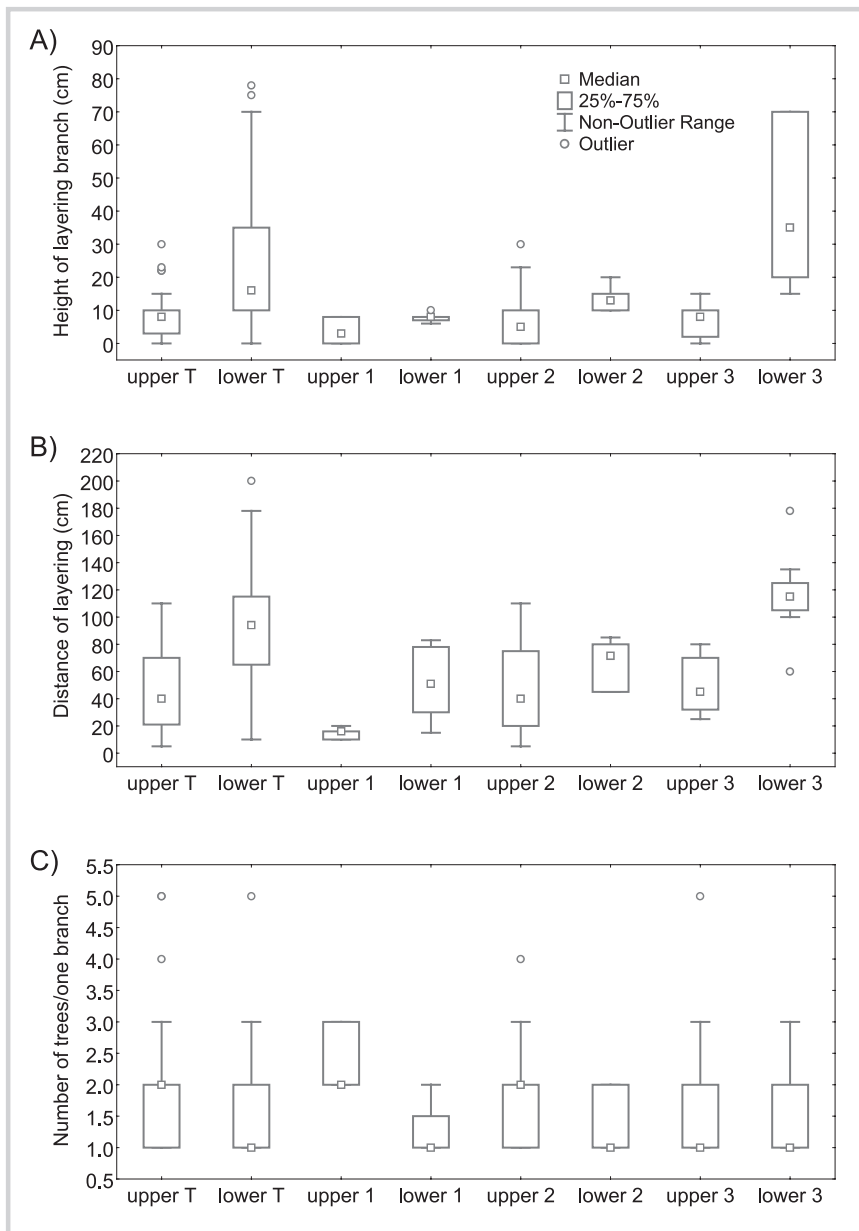

SE2m; Vysoká Hole NW2m; Vysoká Hole SE2m) was similar to Keprník as well. The highest number of specimens was always found in the youngest age class, but their relative proportion was not highly significant (42–53%) (Figure 3).

Discussion

According to Harsch and Bader (2011), 4 types of natural timberline are distinguished; these are determined by different factors. The study area most resembles the "diffuse form" of timberline, its main determining factor

is temperature conditions. However, Harsch and Bader (2011) did not study mid mountains of central Europe, where the timberline is often only conditioned by human activities, as proven by Treml et al (2006) and Novák et al (2010). The distribution of numbers of living specimens in model age classes in the upper RP (Figure 3) and, at the same time, the very low mortality (2.9%) showed that the spruce population here was in the stage of growth (Odum 1983), which is also proven by the lower degree of coverage (1.6%) and the hectare number of all living specimens in comparison with the lower RP. In the lower RP, the growth of the population is decelerating. The

FIGURE 5 Distribution of the directions of layering: (A) lower RP; (B) upper RP.
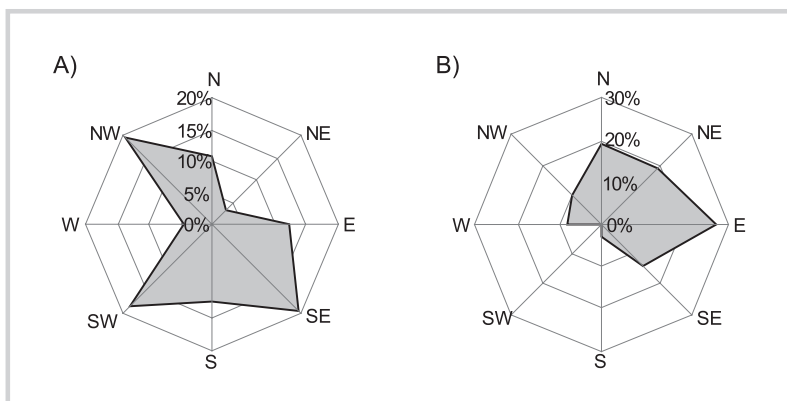
proportion of specimens in the youngest age class was not the highest here, and the stand is gradually closing (degree of coverage, 10.8%). The difference in the age structure between the lower and upper RP can be explained by a gradual increase of the ATLE. The same trend of the timberline shift, determined on the basis of the differences in age structures, was established in all locations of the CPs (Figure 3).

The highly dynamic and intensive height increment is proven by the fact that, within 4 vegetation periods, the original upper line of 5-m-tall spruce, as defined by Treml (2007), was exceeded by 27 specimens, and the original upper limit of 2-m-tall spruce, as defined by Treml (2007), was exceeded by 57 specimens. The upper line of 2-m-tall spruce was not recorded because specimens taller than 2 m were found in the highest part of the RP.

We also observed the ability of the spruce population to take up new spaces by generative specimens (25 specimens per hectare in the lower RP, 39 specimens/ha in the upper RP), even in the highest part of the RP. The occurrence of seedlings was also recorded in all CPs, which reached values similar to the RP (20 specimens/ha, the average value of CPs from the area of the upper line of 2-m-tall spruce trees; 16.7 specimens/ha, the average value of CPs from the area of the upper line of 5-m-tall spruce trees). These were seedlings that had already outgrown the grass–herb vegetation and were more than 4 years of age, which means they had survived the critical life stage after which mortality is reduced to less than 1% (Mellmann-Brown 2002).

The success rate of seed-based regeneration can be affected by the trampling of the vegetation cover by deer, a process that initiates the consequent wind erosion of vegetation (Holtmeier and Broll 2010) and thus supports the creation of a suitable seedbed. In a closed grass–herb vegetation community (*Calamagrostis villosa*, *Nardus stricta*, *Vaccinium* spp, *Luzula* spp) outside disturbed areas, seed germination, and the survival of seedlings are difficult (Šerá et al 2000; Maděra 2004). In 2009, only 27 cones/ha in the lower RP and 0 cones/ha in the upper RP were

recorded, whereas the numbers in 2008 were significantly higher (lower RP, 650/ha; upper RP, 19/ha). In timberline conditions, spruce produces good seed crops once in 9 to 11 years (Tschermak 1950). The considerably lower potential of seed-based regeneration in the upper RP than in the lower RP can be explained by the worse climatic conditions (Traquillini 1979; Holtmeier 2009) and the lower average age of the spruce subpopulation, and thus by the lower number of fertile specimens. Tjoelker et al (2007) report that more abundant flowering, coupled with a substantial production of mature seeds, in open-grown trees in Bosnia occurs at 25 years but not at the alpine timberline ecotone, where the specimens start to be fertile later (Traquillini 1979).

Whether and to what extent the current increasing tendency of the ATLE is related to the increase in temperature in the vegetation periods of the past 2 decades (Houghton et al 2001) cannot be assessed because of the long-term anthropogenic influence on the ATLE in the Hrubý Jeseník Mountains in the past (Hošek 1973; Novák et al 2010). Good seed-based regeneration of spruce is characteristic of pastoral timberline that has been artificially lowered in the past (Plesník 1971; Kozak et al 1995). According to Holtmeier (2009), viable seeds are located below the physiological limit of tree growth. In the present study, viable seeds were found to be present in the highest areas of the RP, high above the current upper treeline (upper line of the trees). We can conclude that this is not a natural position of the upper treeline but an artificially lowered one; and, now, as a result of several decades of spontaneous succession in the reserve, it is being reformed. Although it has been scientifically substantiated (Treml et al 2006, Novák et al 2010) that the timberline in the study area was lowered artificially, we cannot exclude the concurrent influence of temperature amelioration on the appearance of cones and timberline ascent (Baker et al 1995).

On many previous alpine pastures in Europe (eg the European Alps, the Carpathian Mountains), natural tree invasion can also be observed, and, in the long term, a

FIGURE 6 (A) Spruce expanding above the former pastoral timberline; (B) the clonal group in which 3 generations of clonal trees were recorded. (Photos by Martin Šenfeldr)

gradual natural forest advance to the potential climate limit might be expected if grazing and other kinds of use are excluded (Holtmeier 2009). The advance of timberline to higher altitudes, both as a consequence of the end of grazing and global change, would cause the fragmentation and reduction of Alpine forest-free land (Holtmeier 2009). The risk of fragmentation or complete loss of arcto-alpine grounds is, in the case of the Hrubý Jeseník and other Hercynian mid-mountains of central Europe such as the Vosges, Harz, and Kralický Sněžník Mountains,

strengthened by the fact that these small, isolated areas are located near the current anthropogenically influenced timberline (Tackenberg et al 1997, Treml at al 2006, Novák et al 2010). An important role in the current ecotonal dynamics in the Hrubý Jeseník Mountains is played by the natural absence of dwarf pine and other competitively effective edificators (Rybníček and Rybníčková 2004), which do not prevent the expansion of spruce (Figure 6A). On the plots we analyzed, spruce was often present in close proximity to patterned ground; therefore, we can expect its degradation as a consequence of the disruption by the root system (Treml and Křížek 2006). The negative effect also can be expected if spruce grows in arcto-alpine vegetation, as was often found, because this alpine vegetation is then displaced and the properties of the ecotope are changed. Upward shift of the timberline would also reduce landscape diversity, which might affect aesthetic values and would thus have negative consequences for the economy (Holtmeier 2009).

Because of the limited seed-based regeneration under conditions found at timberline, vegetative regeneration seems to be very important (Kuoch and Amiet 1970). Although a specimen of seed-based origin will die, clonal groups may continue to exist indefinitely, as long as the climate does not prevent vegetative growth (Holtmeier 1993). In our RP, 3 generations of clonal origin trees were found (Figure 6B) in the lower section but only 2 generations in the upper section, which can be explained by the overall lower age of the population in the upper RP (Figure 3). The question remains how the original parent specimens, the founders of clonal groups, came to these places. They can be seen as remnants of the afforestation of abandoned pastures (Maděra 2004) or as generatively rejuvenated specimens that further propagated in a vegetative way.

The values of the distance of layering branch rooting and the height of its position in the parent tree are considerably higher in the lower RP, which can be explained by the fact that, in the upper RP, the vegetative regeneration occurs with younger trees and with a higher intensity (a higher amount of layers originating from one branch, a higher number of layers per one primary parent tree). Vegetative regeneration increases with altitude (Holtmeier 1999), which is probably caused by a stronger influence of stress factors in the "summit phenomenon" (wind exposure) (Scharfetter 1918). Breaks and injuries are processes that activate the development of bottom plagiotropic branches and the formation of adventitious roots (Kuoch and Amiet 1970; Brown 1974). When the apical shoot is damaged (frost, drought, abrasion, mechanical damage), plagiotropic branches can elongate vigorously because they are not controlled hormonally by the leader (Holtmeier 2009). The fine root biomass and the ratio of fine root/stem biomass greatly increased with the timberline ecotone altitude; it is considered to be a mechanism for coping with unfavorable soil conditions (Hertel and Schöling 2011).

On the basis of the distribution of the rooting directions, which is perceived as a long-term indicator of wind conditions (Griggs 1938), we can state that wind conditions are of a different character in the 2 sections. In the lower, less-exposed section, there are dominant clonal groups that have a circular shape in a horizontal cross-section, and layering occurs in various directions, which, according to Griggs (1938), indicates no wind influence at a site on horizontal terrain. In the upper RP, which is more noticeably affected by the "summit phenomenon" (Scharfetter 1918) and more exposed to the direct impact of winds, layering is considerably limited by southerly winds, which attain the highest speeds and frequency, especially in winter (Sobíšek 2000). The direction of the flag spruce crowns in the summit areas of Keprník shows that the main devastating attack on treetops has come from the south and southwest.

Conclusions

In the Hrubý Jeseník Mountains, which represent mid mountains of central Europe, the shift of timberline ecotone into higher altitudes was ascertained based on the differences in age structures of spruce populations in different parts of the timberline ecotone. The vegetative form of regeneration of spruce was determined in the studied area. We found up to 3 generations of clonal trees. The intensity of the vegetative regeneration within the timberline ecotone increased with the altitude. We also determined seed-based regeneration, which appears even in the topmost parts of the timberline ecotone. Viable seeds were found even above the current upper treeline.

The ascertained ascent of the timberline ecotone is a result of a decades-long effect of natural processes and the absence of the anthropogenic influence provided by the protection regime of the national nature reserves. This rise in timberline thus has become a significant phenomenon that deserves the increased attention of scientists.

However, the highest areas of Praděd, Vysoká Hole and Keprník, within the Hrubý Jeseník Mountains, are the only locations where the patterned ground and wind-blown alpine grassland with arcto-alpine species are to be found. Their spread probably expanded in the past because of anthropogenous extension of forest-free areas. These arcto-alpine phenomena are among the most significant subjects of nature protection today. Currently, some trees are growing near these phenomena, which affects them negatively. If the natural succession provided by the status of the national nature reserves continues, we can expect the fragmentation of these biotopes, further diminishing the area with a consequent decrease in diversity. Soon, the nature protection authorities will have to decide whether to protect natural processes or significant biotopes often conditioned by historical management and the subsequent successional processes.

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