Development and dynamics of mountain spruce (*Picea abies* [L.] Karsten) stand regeneration

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ABSTRACT: We summarized development and dynamics of natural regeneration in mountain spruce forests in areas affected by bark beetle gradation in the Šumava National Park. Detailed measurements of the regeneration were carried out using Field-Map technology (www.fieldmap.com) on ten permanent research plots. Research plots included the forests with decaying tree layer, stands in partial decline and stands with a generally healthy, or only partially damaged tree layer. Differences in rates of regeneration are very significant between the particular types of plots, especially in the youngest age class. Differences are also evident in the seedling height under varying treatments. The highest numbers of recruits (9,880 per ha) were found under intact overstorey canopies, while the fastest height growth occurred on clearcuts. This study also investigated and evaluated artificial regeneration done in the past.

Keywords: spruce regeneration; Šumava Mts.

Regeneration processes and their dynamics have a great impact on the stability and functional efficiency of forest stands. Due to management restrictions in ecologically sensitive areas, natural regeneration, especially its age, species and height structure, plays a crucial role during the tree layer restoration in forest ecosystems.

Spruce forests are typical of the Šumava Mts. (Sofron 1980). However, bark beetle disturbance has affected the majority of spruce stands at the upper elevations of Šumava National Park (NP) over the last two decades (Vacek et al. 2012). The overstorey tree layer of most maturing and mature mountain spruce stands in declared non-intervention areas has died because of intensive attacks by the eight-toothed spruce bark beetle (*Ips typhographus*), at the beginning mainly at Modravské slatě locality. Only a few vital full-grown spruce (*Picea abies*) trees per hectare have remained in the affected stands (Krejčí et al. 2013).

In natural and near-natural forests, regeneration development is associated with the intensity and frequency of disturbances. Successful natural regeneration depends on a number of factors, particularly light availability, intraspecific competition and competition from other plants on the forest floor, this last factor causing high mortality of spruce within 4–5 years of germination (Canham et al. 1990; Zatloukal 2000; Grassi, Bagnaresi 2001; Jonášová, Prach 2004; Vávrová et al. 2004).

Many factors can influence regeneration success, most notably microrelief (Diaci 2002; Kuuluvainen, Kalmari 2003; Štícha et al. 2010). Other factors are also influential, including sufficient moisture content (Kozlowski 2002). Due to variable climatic patterns at higher elevations, light and warmth are usually limiting factors in climax spruce stands, influencing the competition with other plants as well (Jonášová, Prach 2004; Ulbrichová et al. 2006). Other limitations include overstorey density and composition, frost, and snow movement. The most successful seedling regeneration has been found on dead wood while

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it is much less successful among dense fern cover (*Athyrium distentifolium* and *Athyrium filix-femina*), in grasses (*Calamagrostis villosa*), at more moist localities and in blueberry stands (Remeš et al. 2009).

The aim of this study is to evaluate the character and the development of regeneration on 10 transects in stands attacked by the bark beetle in different residual overstoreys and site conditions.

MATERIAL AND METHODS

This paper deals with the regeneration of spruce stands affected by bark beetle disturbance in the Modravské slatě locality in the Modrava working plan area. The extensive disturbance occurring in this area was a result of the temporal and spatial concurrence of several site and stand factors. The research sites are located in largely even-aged 130+ years old spruce stands, which were planted for the most part in 1860–1870 after severe disturbances. These mountain spruce stands without sanitation measures died over a short interval of time as a consequence of bark beetle attack. According to forest management records (FMR), some sites were clearcut and planted in 1996–2002, whereas on other sites, Norway spruce (*Picea abies*), rowan (*Sorbus aucuparia*), sycamore maple (*Acer pseudoplatanus*) and European beech (*Fagus sylvatica*) were planted beneath the standing dead overstorey, Table 1. Therefore, this study will evaluate the combined (natural and artificial) regeneration in the non-intervention area concerned.

Study was installed on 10 permanent research plots (PRP) located in non-intervention areas in mountain spruce forests nearby the Březník area (Fig. 1). The plots were distributed as follows:

– in forests with standing dead trees and no post-mortality salvage; in recent years standing dead trees were mostly toppled by windthrow, and therefore the bulk of the woody biomass is accumulated on the ground level (forest with dead tree layer), PRP 1, 2, 3, 7, 8, 9.
– stands subjected to sanitation where the stems infested by bark beetles were left after debarking in the forest or they were hauled away for processing (clearcut), PRP 4, 5, 6.
– healthy (at least temporarily) forest stands or forest stands that have been partially affected by the bark beetle feeding where regeneration takes place under the shelterwood of parent stand, PRP 10.

PRP were divided into three different groups based on similar site conditions:

PRP 1, 2, 3. Situated on the western slope of Velká Mokrůvka Mt. at an altitude of 1,200–1,300 m a.s.l., slope 30°, the stand has been left without in-

Table 1. Characteristics of particular PRP and numbers of recruits from the last measurements taken in 2010

PRP		Plot condition	Stand and age at stand disintegration	Altitude (m a.s.l.)	Exposure and growing stock at disintegration ($m^3 \cdot ha^{-1}$)	Forest site type	Cover E_1 and species dominance (%)	Total number of recruits (trees·ha⁻¹)	Artificial regeneration from FMR (trees·ha⁻¹)
1	Velká Mokrůvka	dead tree layer	55B5/1 150 years	1,200	W 304	8O1	85 Calvil 40, Avefle 35	5,920	1,574
2		dead tree layer	55C4/1 164 years	1,260	W 356	8K3	80 Calvil 40, Athdis 25	3,360	517
3		dead tree layer	55C4/1 164 years	1,300	W 356	8K3	85 Calvil 45, Avefle 30	19,760	517
4		clearcut	55B2	1,200	W	8K3	90 Calvil 50, Avefle 30	2,800	1,574
5		clearcut	55B2	1,240	W	8K3	90 Calvil 60, Avefle 20	2,280	1,574
6		clearcut	55C2	1,300	W	8Y1	90 Calvil 65, Avefle 15	6,960	517
7	Pytlácký roh	dead tree layer	76F2 149 years	1,240	N 334	8K7	80 Calvil 50, Avefle 20	2,720	3,199
8		dead tree layer	76F2 149 years	1,250	N 334	8K7	80 Calvil 50, Avefle 20	2,640	3,199
9		dead tree layer	80A3 134 years	1,260	N 295	8K7	85 Calvil 55,Avefle 20	1,520	2 268
10	Povalová cesta	forest with living tree layer	69A5 128 years	1,120	flatland 404	8K78R1	80 Vacmyr 45, Lycann 20	9,880	0

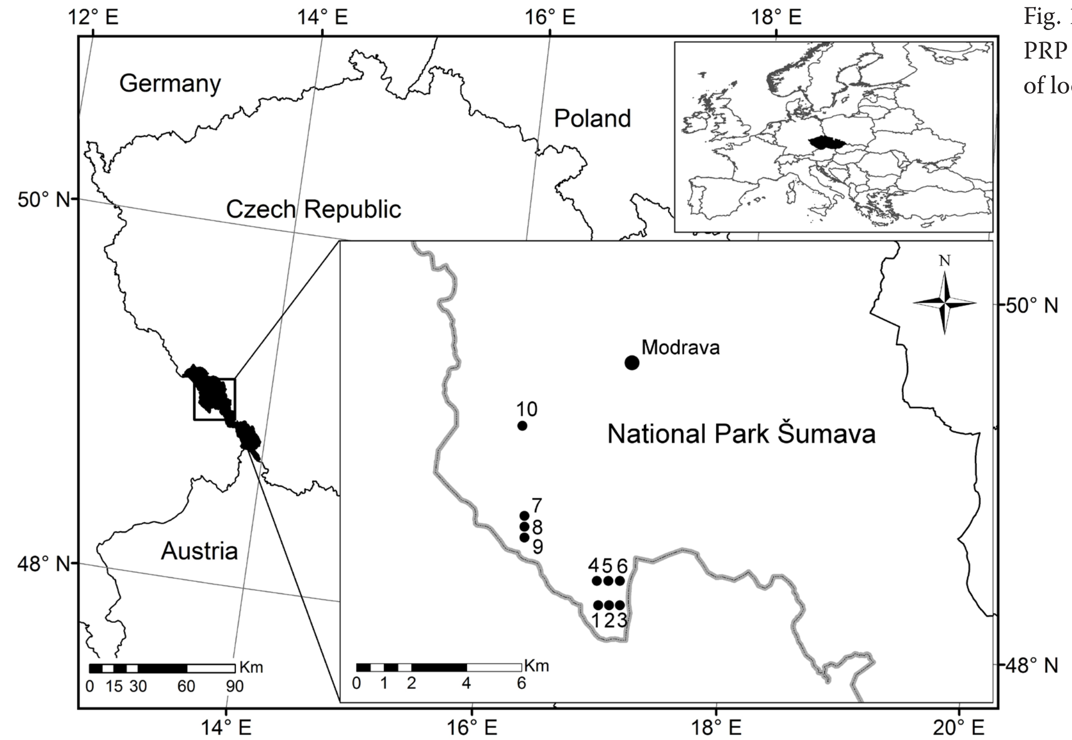

Fig. 1. The situation of PRP in Modrava, map of localities

tervention against the bark beetle since 1995. The average age of spruce at the time of mortality was 150+ years.

PRP 4, 5, 6. Also situated on the western slope of Velká Mokrůvka Mt. at an altitude of 1,200–1,300 m a.s.l., 30° slope. These PRP are located on clearcuts, above each other along the fall line, in a similar horizontal plane of the slope like PRP 1, 2, 3. The parent stand was felled and cable skidded after the bark beetle attack and timber was hauled away. These clearcuts were reforested mostly with Norway spruce and rowan,

PRP 7, 8, 9. Situated on the northern slope of Blatný vrch Mt., in the Pytlácký roh district, above each other along the fall line at a height of 1,240 to 1,260 m a.s.l., slope 25°. In the years 1994–1998 when severe bark beetle attacks occurred, no interventions were made against the bark beetle. As a result, the spruce parent stand died at an age of about 150 years. Currently, disintegration of the standing dead trees is under way and suitable conditions for weed expansion have been created. Finally, PRP 10 is situated behind the Roklanská Chalet near Povalová cesta (Corduroy Road) in a stand with relatively differentiated structure, with a lower stocking than in the other plots of this study, stand age of 128 years and the proportion of spruce approximately 10%. This transect is located at an elevation of 1,120 m a.s.l. The stand is in Zone II of the National Park, where in 2007 the site was included in the newly created non-intervention management system. Because of this new designation, there has been no treatment for the bark beetle since 2007, in adjacent stands the Kyrill hurricane caused windfalls while spruce windfalls were recorded also on PRP 10.

All research plots are mostly in forest site type groups 8K, 8Y, 8R, 8O (Viewegh et al. 2003). The herb layer is dominated by *Calamagrostis villosa*, *Vaccinium myrtillus*, *Avenella flexuosa* and *Luzula sylvatica* are also present. The soils are skeletal, sandy-loam, acid to strongly acid modal Podzols and Cryptopodzols. The prevailing soil type in the Velká Mokrůvka locality is Ranker Podzol, at the foothill it is Pseudogley Podzol. The parent rock is composed of granite and granodiorite. Average annual precipitation is approximately 1,400 mm and average annual temperature is 3.5–4.5°C.

The intent of transects was to characterize the average abundance and maturity of regeneration. On each PRP one transect 50 × 5 m in size (250 m^2) was marked out and stabilized. Regeneration measurements included all recruits present in the particular transects whose diameter at breast height was less than 5 cm. All positions, height, increment, browsing damage and tree species of regeneration were measured during autumn, after the growing season. The number of recruits (up to 100 cm), species composition and the share of damaged individuals were described by relative proportion. The height of recruits was summarized in Table 2 by mean and standard deviation.

The growth of a new tree generation was analysed in detail on PRP 1 to 6. The height and annu-

Table 2. Mean heights and standard deviations of Norway spruce recruits on PRP (in cm) in 2002–2010

PRP	2002	2003	2004	2005	2006	2007	2008	2009	2010
1	40.8 ± 27	53.2 ± 31	63.0 ± 34	75.6 ± 40	92.9 ± 46	112.8 ± 56	134.5 ± 69	156.6 ± 81	184.4 ± 96
2	22.2 ± 21	28.1 ± 24	35.7 ± 26	41.8 ± 28	56.5 ± 32	74.5 ± 39	89.0 ± 47	107.0 ± 55	129.9 ± 68
3	16.1 ± 12	22.5 ± 16	30.5 ± 20	33.7 ± 23	45.6 ± 30	54.8 ± 33	66.8 ± 39	80.2 ± 45	105.3 ± 49
4		179.1 ± 109	207.0 ± 123	229.7 ± 135	249.2 ± 145	272.0 ± 164	302.1 ± 177	331.7 ± 188	355.0 ± 201
5		135.4 ± 96	161.7 ± 112	183.5 ± 126	207.6 ± 143	223.4 ± 159	254.1 ± 173	284.4 ± 187	319.1 ± 196
6		69.8 ± 51	84.2 ± 58	94.8 ± 62	108.2 ± 66	125.7 ± 79	142.2 ± 90	160.7 ± 104	179.8 ± 117
7	68.6 ± 33	89.0 ± 38	105.7 ± 45	117.8 ± 51	131.3 ± 65	164.3 ± 88	198.7 ± 108	221.5 ± 122	
8	46.3 ± 32	63.1 ± 39	77.6 ± 42	95.3 ± 54	114.2 ± 59	135.0 ± 71	160.3 ± 85	182.0 ± 95	
9	15.5 ± 12	23.3 ± 16	32.8 ± 34	40.0 ± 31	54.1 ± 34	63.0 ± 32	74.7 ± 33	86.2 ± 37	
10	41.1 ± 47	44.6 ± 48	35.5 ± 51	38.7 ± 54	43.0 ± 56	37.9 ± 41	40.4 ± 41	40.0 ± 43	

al height increment were compared according to the type of plot (planting on clearcut area, underplanting and natural regeneration in dead forest stand) and the position within the slope. Analysis of variance was used for testing differences between the plots by STATISTICA 12 (SPSS, Tulsa, USA).

RESULTS

PRP 1, 2, 3 – Velká Mokrůvka

Norway spruce accounts for 97% of all regeneration on the PRP. Rowan and silver birch are also present. The plot with the highest number of recruits, PRP3, contained 19,760 trees·ha^{-1} in 2010, out of which spruce recruits represented 94%, rowan recruits 5% and birch recruits 1%. On PRP 2 the average number of recruits in 2010 was 3,360 trees·ha^{-1}, which was a lower number of recruits, probably due to a higher incidence of ferns that inhibited regeneration. On PRP 1 the average number of recruits from combined regeneration was 5,920 trees·ha^{-1}. During previous measurement periods, slightly higher numbers of recruits were recorded; this decrease in the number of recruits is a result of natural self-reduction and herbivory from game. Across all plots, 62% of broadleaved species displayed evidence of damage by game; this factor limits the high increment. The frequency of spruce recruits in height classes is illustrated by a histogram of height classes in 2004, 2006, 2010 (Fig. 2a). In 2010 the average height of spruce recruits (combined regeneration) on these plots was 128.6 ± 59 cm while the tallest spruce recruit reached the height of 508 cm and the shortest recruit measured 11 cm. Table 2 shows the average heights of spruce recruits in 2002–2010. In 2010 the naturally regenerated trees taller than 100 cm accounted for ca 55% of regeneration. According to FMR, artificial regeneration (underplantings) in forest stands on PRP 2 and 3 of spruce amounted to 517 trees·ha^{-1} in 1995–1998. In a forest stand on PRP 1, the reported underplantings of spruce were 1,037 trees·ha^{-1} and those of rowan amounted to 537 trees·ha^{-1} in 1995–2001.

PRP 4, 5, 6 – Velká Mokrůvka

Norway spruce accounts for 100% of the species spectrum of regeneration on PRP 4, 5, 6; broadleaves were found sporadically on these plots in 2006, severe browsing damage by game was observed in stands of broadleaved species. In the course of measurements in 2010, we found no broadleaved species on these plots. The average number of spruce recruits on PRP 4 in 2010 amounted to 2,800 trees·ha^{-1}, compared to 2,280 trees·ha^{-1} on PRP 5 and 6,960 trees·ha^{-1} on PRP 6.

The frequency of spruce recruits in height classes in 2004, 2006 and 2010 is illustrated in Fig. 2b. In 2010 the average height of spruce recruits on these plots was 243.3 ± 176 cm; the tallest spruce reached the height of 770 cm while the smallest recruit was 22 cm.

In 2010, the recruits from combined regeneration taller than 100 cm (biologically established ones) accounted on average for 80% of all recruits. The recruits are large enough to resist browsing and competition by weeds. However, they often suffer damage by snow and frost; damage was recorded in

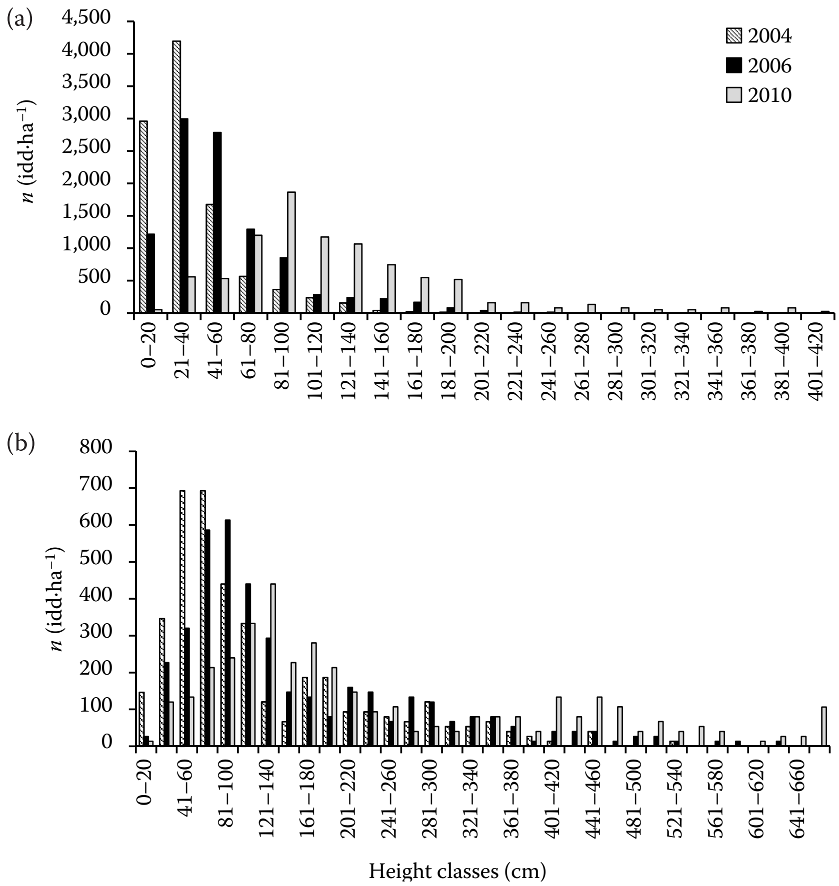

Fig. 2. A histogram of the height structure of recruits from combined regeneration on (a) PRP 1, 2, 3; (b) PRP 4, 5, 6

15% of trees. According to FMR from 1995–2001, 1,037 spruce trees·ha^{-1} and 537 rowan trees·ha^{-1} were planted in these stands on PRP 4 and 5. A total of 517 spruce trees per ha were planted on PRP 6 from 1995 to 1998.

PRP 7, 8, 9 – Blatný vrch

Norway spruce accounts for 91% of the combined regeneration on these plots; other species are rowan and sycamore maple. In 2009 the average numbers of recruits on PRP 7 were 2,720 trees·ha^{-1} of spruce combined regeneration. On PRP 8 the average number of spruce recruits in 2009 was 2,640 trees·ha^{-1} in total. On PRP 9 the average number of recruits in 2009 was found to be 1,520 trees·ha^{-1}. In 2009 the average height of spruce recruits on these plots was 190.1 ± 126 cm and the tallest spruce reached the height of 472 cm while the lowest tree measured 15 cm. In 2009 the recruits taller than 100 cm (biologically established ones) accounted on average for 61% of all recruits. The recruits are mostly tall enough to resist weeds and browsing.

On average 1,012 spruce trees, 1,983 rowan trees and 144 sycamore maple trees per ha were underplanted on PRP 7 and 8. According to FMR, on average 731 spruce trees, 537 rowan trees and 1,000 sycamore maple trees per ha were reported as underplantings on PRP 9. The frequency of spruce recruits in height classes is documented in a histogram of height classes in 2004, 2006, 2009 (Fig. 3a).

PRP 10 – Povalová cesta

Out of 9,880 trees·ha^{-1} measured on this PRP in 2009, Norway spruce and rowan accounted for 92.3% (9,120 trees·ha^{-1}) and 7.7% (760 trees·ha^{-1}) of the species spectrum of regeneration, respectively. In 2006 the average number of recruits in this transect was 8,680 spruces per hectare and 520 rowans per hectare from 2006 to 2009; both the total number of rowans and the percentage of total regeneration in rowans increased, as did evidence of browsing damage caused by game. In height classes up to 60 cm, the largest portion of spruce recruits came from new seedlings (causing the exponential decline in the histogram, Fig. 3b). In 2009 the mean height of spruce recruits was 40 ± 43 cm and the tallest spruce tree reached the height of 242 cm while the shortest was measured at 3 cm. In 2009

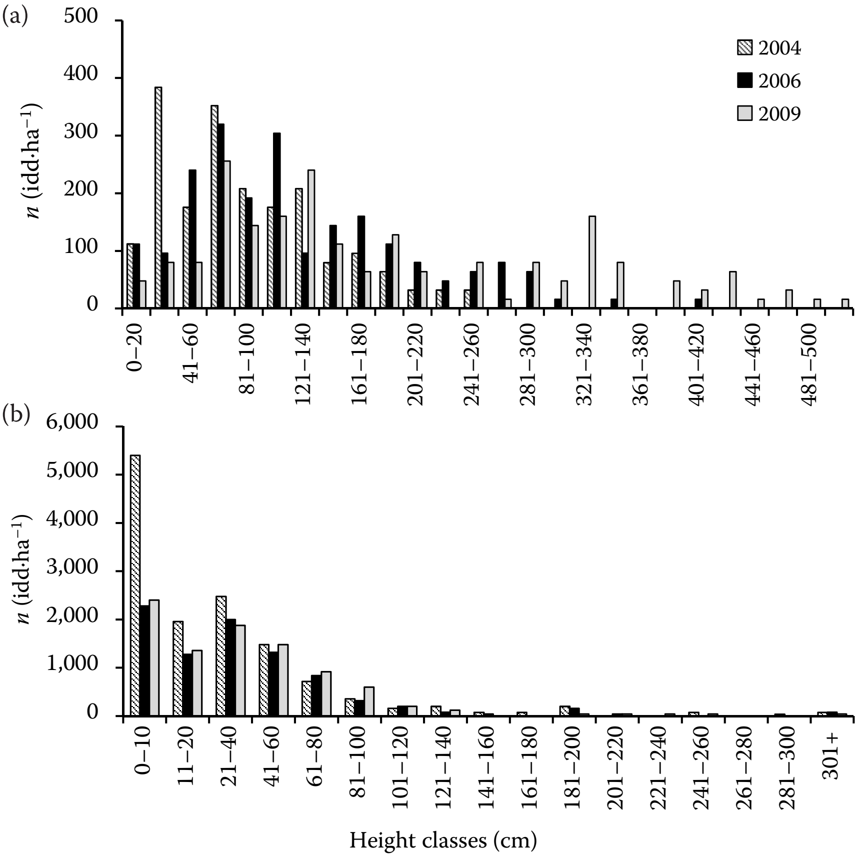

Fig. 3. A histogram of the height structure of recruits from combined regeneration on (a) PRP 7, 8, 9; (b) PRP 10

the recruits taller than 100 cm accounted for only 5% of all recruits.

The height structure of natural regeneration on the plot with the vital tree layer is significantly different from that on the plot with declined forest and from the height structure of regeneration on clearcuts.

Comparison of plots

The average height and annual height increment in 2004 on permanent research plots 1–6 are shown in Figs 4 and 5. Analysis of variance confirmed statistically significant differences in mean height in 2004 between research plots [$F(5, 626) = 107.82$, $P = 0.0000$, Fig. 4]. Only plots 2 and 3 did not differ significantly in the heights of the trees, neither did plots 1 and 6.

The situation was very similar in the case of annual height increment [$F(5, 626) = 35.693$, $P = 0.0000$, Fig. 5]. The height growth of young trees on clearcut sites was significantly faster compared to the young trees growing under standing dead trees. In both types of plots, the tree growth was faster in the bottom part of the slope, due to better soil and temperature conditions.

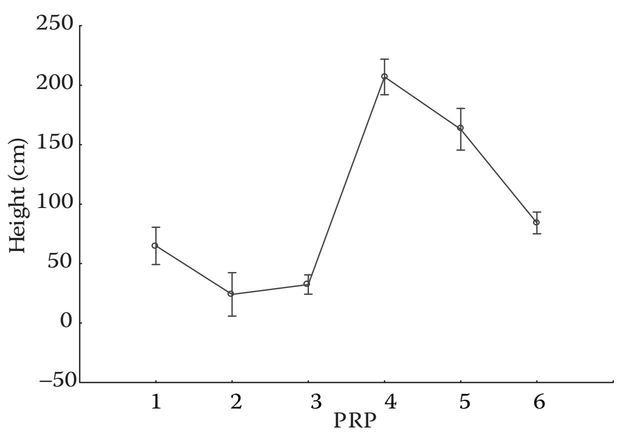

Fig. 4. Mean height on the PRP in 2004

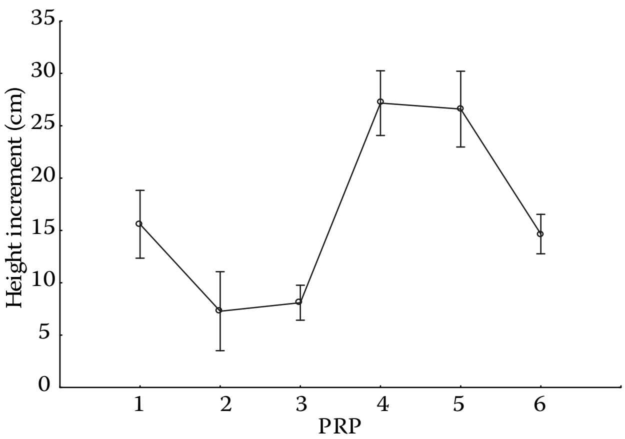

Fig. 5. Height annual increment on the PRP in 2004

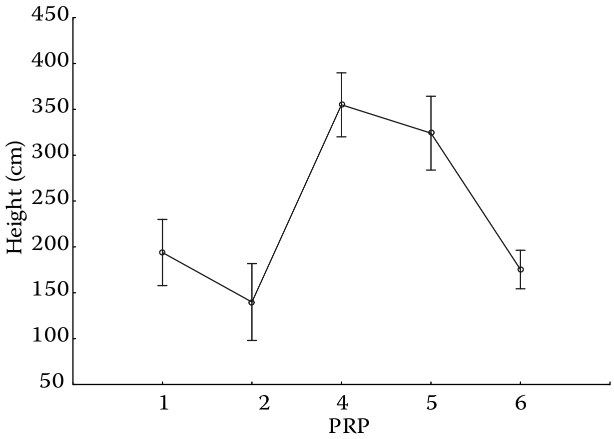

Fig. 6. Mean height on the PRP in 2010

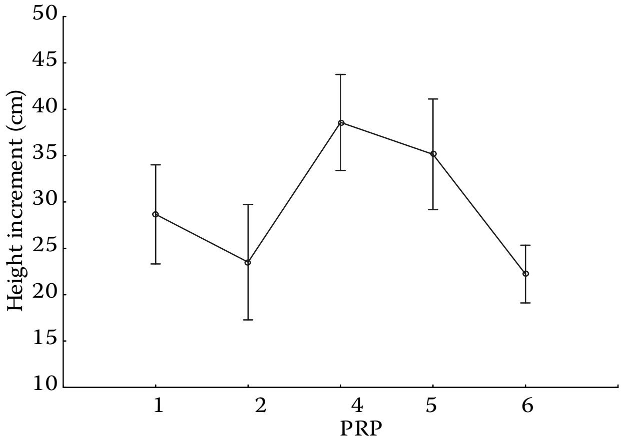

Fig. 7. Height annual increment on the PRP in 2010

The situation was similar in 2010, yet the significance of difference in mean height between the plots slightly decreased [$F(4, 395) = 29.297$, $P = 0.0000$, Fig. 6]. Analysis of variance confirmed significant differences only between PRP 4, 5 and the other plots.

This trend is apparent also when comparing the height annual increment in 2010 [$F(4, 395) = 29.297$, $P = 0.0000$, Fig. 7], where significant differences were proved only between pairs of plots: 4 and 6; 5 and 6; 4 and 2.

DISCUSSION

The numbers of spruce recruits recorded on all studied plots are sufficient to ensure the existence of a new generation of mountain spruce stands. Korpeľ et al. (1991) estimated that the required minimum number of recruits 50–130 cm in height should be 150–200 trees·ha^{-1}. This number has been exceeded many times on all studied plots. For successful regeneration (defined as a sufficient number of seedlings needed for creating the new mature tree layer), it is essential that there are sufficient numbers of seeds and seedlings in the forest stand before disturbance (Fischer 1992). If this sufficient, pre-disturbance inventory exists, then the recruits can react by increasing height increment after breaking the canopy (Canham 1989).

On the other hand, Nilsson et al. (2002) found that the mortality of seedlings was higher if there was a rapid change from live forest structure to clearcut due to a dramatic change in the microclimate. However, a reduced canopy caused by wind-damage breaking of the overstorey stems can encourage the growth of seedlings because of higher light and moisture availability (Drobyshev 2001). Small disturbances (stem breakage on small plots), particularly in even-age, large forest stands, are the opportunity to create the varied forest structure (Zukrigl 1991). On large clearcuts and plots with a dead tree layer (with downed trees in combination with standing dead trees), the number of the youngest seedlings is limited (Figs 2 and 3a) and after that we can expect the formation of an even-aged structure (compared to a forest with small disturbed plots). Jonášová (2001, 2004) described the high variability in the amount of seedlings and their height structure, our results documented a decrease in the number of the youngest seedlings on large disturbed areas and the more so on large clearcuts.

The number of recruits on our PRPs was highly variable (about 1.5–19.7 thousand trees·ha^{-1}), which is in accordance with Zatloukal et al. (2001), where about 6–17 thousand trees·ha^{-1} were observed in spruce stands in Šumava.

Nevertheless, for the evaluation of natural seeding viability the influence of game and other factors must be taken into account (Gubka 2006). Besides the repeated damage to interspersed broadleaves caused by game browsing, local damage to recruits caused by the fall of standing dead trees previously attacked by bark beetles has been observed in recent years.

CONCLUSIONS

The number of trees in the youngest age class was most closely related to the number and proximity of live parent trees in the overstorey. Therefore, on plots with living parent stand, the values in this category are usually significantly higher than the number of recruits in stands with a dead tree layer or on clearcuts.

Besides quantitative differences, we also found differences in the height structure of recruits between these two types of sites. They are related not only with the replenishment of recruits in the youngest age category but also with the light regime, which is more beneficial on plots with a sparse or non-existent overstorey, allowing for higher increments. The average height of spruce recruits on the studied plots ranged from 20 cm (on plots with living parent stand) through 65 cm on plots with a dead overstorey to more than 130 cm on clearcuts. This difference is caused not only by higher increments on less sheltered plots but also by a higher percentage of the youngest recruits on plots with living stand, which significantly reduces the average height.

A graph of the frequency of height classes of recruits has the shape of the Gaussian curve at sites with dead parent stand while in forests with live trees in the overstorey, it has the shape of the negative exponential. This is conditioned by recruitment of seedlings due to the continuous natural regeneration. The height class above 100 cm is the most numerous on clearcuts due to the faster growth of thickets whereas the lowest height class (0–20 cm) is not represented at all.

Artificial regeneration on clearcuts is characterized by taller heights of stands, larger variance of heights and lower total number of trees compared to plots with standing dead trees. As water is not limiting on these sites, these results are likely due to the faster growth of spruce on bare plots where full saturation is ensured by solar radiation. In recent years, severe damage to particular trees caused by snow has been observed that is connected with tree bending, breaks and stem deformations.

There are no distinct differences in the spatial structure of recruits between stands with living and dead tree layer, which ensues from the preference of suitable microsites by mostly natural regeneration and subsequent differentiated survival of seedlings. This process results in the clustered nature of recruits at the stage of natural seeding and advance regeneration. In this respect artificial regeneration behaves in a clearly different way due to the more regular distribution of trees found out on clearcuts.

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