Natural regeneration of acidophilous spruce mountain forests in non-intervention management areas of the Šumava National Park – the first results of the Biomonitoring project

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Abstract

The first results of the Biomonitoring project, a long-term inventory project, which was established in non--intervention areas of the Šumava National Park, a large Natura 2000 site, are published in this paper. A number of parameters were recorded in permanent plots to describe the species and spatial structure of the forest ecosystem in areas with spontaneous succession. Repeated measures are planned to study changes over time and define the factors, which are the most important for natural regeneration of Central European mountain forests. We used similar methods as are applied in the long-term inventory of mountain forests in the Bavarian Forest National Park to be able to compare the results of both inventory projects in the transboundary region. The aim of this study was to investigate the regeneration of mountain spruce forests seriously affected by large-scale disturbances (both windstorms and bark beetle infestation). The mean density of the regeneration was 4,848 individuals per hectare (median 2,960 ind.ha⁻¹) in the whole plots and 7,882 ind ha⁻¹ (median 2,122 ind ha⁻¹) in the small regeneration plots, in which we conducted detailed seedling characteristics surveys. We found that there were enough seedlings and young trees growing in mountain spruce forests in the Bohemian Forest (Sumava in Czech) to guarantee their natural regeneration. There were already many seedlings and young trees occurring in the plots before the large--scale disturbances thus ensuring forest recovery. Our results confirm that dead wood quantity and its quality (level of decomposition, structure, distribution in forest, etc.) are crucial for successful natural regeneration of mountain spruce forest. Dead wood was confirmed to be an important microsite for spruce regeneration. However, only low numbers of seedlings were found on decorticated logs (bark was rubbed off to avoid bark-beetle infection) created during salvage logging operation. While this method was good for suppressing bark beetle, it was not suitable for spruce regeneration. We recommend that the results of this study should be included as a part of post-disturbance forest management activities in mountain forests, not only in national parks.

Key words: Bohemian Forest, Natura 2000, mountain spruce forest, regeneration, dead wood, bark beetle, disturbances

INTRODUCTION

Mountain spruce forests are one of the most important and valuable ecosystems of Central Europe, not only because they cover large areas, but also for delivering numerous ecosystem services. Spruce forests were used mainly for economic purposes in the past, but also their

water accumulation and soil protection functions were highly valued (BRANG 2001, SPIECKER 2003). During the last several decades, their importance for biodiversity protection and nature conservation has increased (KRAUCHI et al. 2000; SPIECKER 2003). Several national parks and a number of natural reserves were established to protect the last Central European mountain forests still only slightly affected by fragmentation and direct human influences.

Natural disturbances, especially windstorms together with bark beetles, often cause large dieback areas in mountain spruce forests (HOLEKSA & CYBULSKI 2001; FISCHER et al. 2002; KULAKOWSKI & BEBI 2004; HOLEKSA et al. 2007; SVOBODA & POUSKA 2008; SVOBODA et al. 2010). A strong natural regeneration is an important guarantee of mountain spruce forest maintenance (HEURICH 2009). Clear cutting and logging of damaged trees negatively affect the natural regeneration rate due to direct destruction of seedlings as well as soil erosion and degradation of soil quality. Various scientific results (i.e., GROMTSEV 2002; FISCHER & FISCHER 2009; JONÁŠOVÁ et al. 2010) show that natural recovery of coniferous forests after wind, bark beetle, or other natural disturbances is important and can be more successful compared to artificial planting of trees. An increasing number of mountain spruce forests growing in nature reserves and core zones of national parks are managed as "non-intervention areas", in which natural disturbances are accepted as an integral part of their development (TURNER et al. 1997; DEMETRY 1998; REICE 2001; FRANKLIN et al. 2007). Sufficient natural regeneration is a key factor for the natural reconstruction of these forests.

Two national parks, the Bavarian Forest NP and the Šumava NP were established in the Bohemian Forest in 1970 and 1991, respectively. These two parks protect together 22,670 ha of mountain spruce forests, one of the largest complexes in Central Europe. These forests have been widely studied, including the study of different ecological aspects during the last two decades (FISCHER & JEHL 1999; PODRÁZSKÝ et al. 1999; ZATLOUKAL 1999; FISCHER et al. 2002; JONÁŠOVÁ 2004; SVOBODA 2007; BAČE et al. 2009; BAUER et al. 2008; FISCHER & FISCHER 2009). A large-scale and long-term investigation of mountain forests' natural regeneration was started in a non-intervention ('natural') zone of the Bavarian Forest NP in 1991 (HEURICH et al. 2010). Repeated investigation has already found a high degree of natural regeneration with good diversity and spatial distribution. Successful recovery of mountain forests in the Bavarian Forest NP after windstorm and bark beetle outbreaks has been confirmed (HEURICH 2009).

In the Sumava NP, the large-scale inventory of mountain forests regeneration started in 2008. The Biomonitoring project is the first project covering a whole non-intervention zone. Methodologies of both inventories are analogous for enabling to compare results from the bilateral national parks sharing the same ecosystem. In the Biomonitoring project, various tree characteristics are periodically recorded in permanent plots with the main goal being to describe species composition and spatial structure of mountain spruce forests together with their dynamics and changes over time.

The Sumava NP is an important Natura 2000 site; the main habitat type categories (CHYT-Rý et al. 2001) were chosen to cluster the permanent plots. In 2008, we started the project by investigating habitat type 9410 - Acidophilous spruce forest, which is the most common habitat in the non-intervention zone of the Šumava NP.

This paper presents the results of the first large-scale monitoring focusing on the natural regeneration of mountain spruce forests in the Šumava National Park. Three main questions are adressed: (1) What are the numbers of seedlings, their species composition and spatial distribution? (2) Are there differences in natural regeneration of mountain spruce forests before and after windstorm and bark beetle disturbances? (3) Which microhabitats are the most important for natural regeneration?

MATERIAL AND METHODS

Site description

The Šumava National Park is located in the southwest part of the Czech Republic, where the the Bohemian Forest (Šumava in Czech, Böhmerwald in German) reaches to 1,378 m a.s.l. and creates a natural border of the Czech Republic with Austria and Germany (Fig. 1). The highest peak (Großer Arber, 1,456 m a.s.l.) is located in Germany, only 5 km south-west of the state border. The Šumava NP (over 68,000 ha) together with its transboundary partner, the Bavarian Forest NP (24,000 ha) on the German side, create the largest strictly protected area in Central Europe.

The geology of the Bohemian Forest is mainly composed of acid rocks: moldanubic with its paragneiss and migmatits and moldanubic pluton with granitoids (LOŽEK 2001). The soils are nutrition poor with cambisols, cryptopodzols, podzols, and organic soils being the most common (KOČÁREK 2003). The cold mountain climate is characterised by an average annual temperature of about 4.2 °C and average rainfall of 1,090 mm (Czech Hydrometeorological Institute – Churáňov station, 1,118 a.s.l.; TOLASZ 2007; http://www.chmi.cz/).

Forests cover over 80% of the Šumava NP and 24% of the forests are managed as nonintervention zones, i.e., no direct human interventions (no logging, tree manipulation, or artificial planting) are applied there.

The Biomonitoring project started with a detailed investigation of the three main types of Natura 2000 'habitat 9410' (Montane *Calamagrostis* spruce forests, Bog spruce forests, and Montane *Athyrium* spruce forests), which together cover 16,827 ha of the Šumava NP. Norway spruce (*Picea abies*), together with mountain ash (*Sorbus aucuparia*) and sycamore (*Acer pseudoplatanus*), are the most common trees in these forests. In the Bohemian Forest, natural mountain spruce forests grow at altitudes above 1,150–1,200 m a.s.l. and in azonal waterlogged and gleyed locations.

Design of data collection

Permanent plots are irregularly distributed within the Šumava NP (Fig. 1), with most concentrated in a few locations: Polom Mt., Plesná Mt., Ždánidla Mt., Třístoličník Mt., Plechý Mt., Smrčina Mt., and uplands around Kvilda and Modrava villages.

A network of randomised points separated by 353.55 meters, formerly established as a network for the Forest Inventory in the Czech Republic and the Large-Scale Inventory of Šumava NP Forests (1998–2003), was used to place the centers of permanent plots: 130 permanent plots were randomly chosen from a total of 470 plots generated for habitat type 9410. Plots were investigated from May to October 2008. Seven plots were reclassified as other habitat types and excluded from the study during the field work.

Permanent plots are circles with the size of 500 m^2 . Field-Map technology (ČERNÝ 2010a) was used to mark the plots in the field and collect the data. Plot centers were located by GPS and also fixed by merestones; two field marks were also used to assure finding the plots for the next investigation. Data on each plot were clustered in seven sections (for database structure, see Table 1).

Data set – Forest regeneration

We recorded in each permanent plot:

(1) The total number of young trees growing in the entire permanent study plot (hereafter reported as PSP). The size of a PSP is 500 m^2 .



Fig. 1. A distribution and regeneration density in the monitoring plots, which were located in the nonintervention zone (area with natural regeneration), in 2008. The radius of each circle shows the category of observed regeneration density. The same categories were used also in Fig. 5.

Table 1. Basic characteristics collected in the monitoring plots.

Layer	Layer characteristics and collected attributes
Plot	Basic plot characteristics: date, altitude, slope, aspect, terrain relief, canopy, stand ID, past management.
Living trees	Position and description of living trees inside 3 concentric circles: tree species, diameter breast height (DBH), height, stem breaks, forks, stem damage, fungi presence, evidence of bark beetle.
Dead trees	Position and description of standing dead trees inside 3 concentric circles: tree species, diameter breast height (DBH), height, stem breaks, forks, fungi presence.
Tree species regeneration	Description of tree species regeneration: plants with height between 0.1 m and DBH 69 mm.
Stumps	Description of stumps smaller than 1.3 m: tree species, diameter class, origin, stage of decay, fungi presence, density of tree species regeneration.
Lying deadwood	Description of lying deadwood (minimal diameter is 70 mm and minimal length is 1 m): tree species, length, middle diameter, origin, stage of decay, surface contact, fungi presence, density of tree species regeneration.
Site	Phytocoenological relevé and proportion of microsites important for tree species rege- neration.

Table 2. Decay stages of lying deadwood and stumps.

Decay stage	Characteristics
1	deadwood is hard; a blade can be struck to a maximum depth of 0.5 cm
2	deadwood is mostly hard, a blade can be struck to the depth 1-2 cm
3	deadwood is partly decomposed, a blade can be struck to the depth 2-5 cm
4	deadwood is mostly soft; the blade can be struck to its full depth
5	deadwood is very soft (during manipulation it disintegrates, the shape of lying deadwood follows the terrain)

(2) Particular characteristics of all young individuals occurring in small detail regeneration plots (hereafter reported as DRP). The size of a DRP is 28.27 m².

Young trees recorded in a PSP were divided into two size categories (10-20 cm and >20 cm high) and two species categories (spruce and other species). Combination of these categories creates four groups of seedlings. Their microhabitat positions were classified as 'laying dead-wood' or 'stump or stub of dead tree'. Degrees of dead wood decomposition (Table 2) were also recorded.

A small DRP is 6 m in diameter and its centre is located 7 m north of the PSP centre. The DRP is used for investigation of seedling density and detailed description of their growing characteristics (Table 3). Seedlings growing on stumps, stubs, decomposed dead wood, or rocks were categorised as 'natural regeneration'. Growth habit of seedlings often helped to distinguish natural regeneration from artificial plantings. Seedlings coming from a nursery usually grow faster, their branches are longer, and they are not as dense as seedlings growing from natural regeneration. Most of the seedlings smaller than 20 cm were recorded as natural regeneration. Also, seedling density and space distribution could help to determine seedling origin. The Czech Forestry Directive recommends 3,000–3,500 seedlings per hectare. Thus, there is a low probability that more than 10 seedlings could be planted in a DRP (28.27 m²).

Young trees growing in lines or dense clusters often indicate a natural origin (ČERNÝ 2010b). Young trees classified as 'artificial planting' occurred mainly close to stumps or stubs, as were trees with individual chemical or mechanical protection. Seedlings of tree

Table 3. Tree species regeneration characteristics collected on the small regeneration plots (28.27 m²).

Characteristics	Attributes
tree species	
height	
DBH	if the tree is taller than 1.3 m
microsite	1 – litter, 2 – litter on the stone or rock, 3 – lying deadwood, 4 – stumps, 5 – grass turf, 6 – other vegetation, 7 – mineral soil
terrain relief	1 - between root swellings, $2 - on the windfall circle$, $3 - under windfall circle$, $4 - other$
origin	1 - natural regeneration, 2 - artificial regeneration, 3 - origin unknown
support	1 – without support, 2 – individual mechanical support, 3 – individual chemical support, 4 – large area fencing
damage type	1 – without damage, 2 – mechanical damage not caused by game, 3 – terminal browsing, 4 – lateral browsing, 5 – fraying, 6 – peeling, 7 – frost damage to current year shoots
damage age	1 - new, 2 - old, 3 - repeated

species missing in the tree layer were also usually classified as artificial plantings. A category 'seedling of unknown origin' was used in unclear cases. Seedling numbers were calculated per hectare.

Two data sets about forest regeneration can partly differ in accuracy. While data from a PSP comes from a brief overview of the large plot, in which a few young trees can be missed or counted twice, a more accurate investigation is applied to the DRPs. All seedlings are investigated in three concentric circles temporarily marked in the field. This avoids missing or double counting of seedlings. On the other hand, due to the clustered occurrence of spruce regeneration in a stand, large plots better cover this spatially non-random occurrence and might give more reliable results.

Data analysis

The same data categories were used to analyze data about forest regeneration from both PSP and DRP: spruce 10–20 cm; spruce +20 cm; spruce ALL; other species 10–20 cm; other species +20 cm; other species ALL. Basic statistical parameters (i.e., mean, standard error of mean, standard deviation, and median) were calculated for all categories.

The total area of lying dead wood (i.e., tree trunks or their fragments laying on the soil surface) was calculated as the sum of the length and diameter of each piece occurring in all plots. The total area of stumps was calculated as the sum of the area of all stumps recorded in the plots. The total area of dead wood was calculated as the sum of the area of laying dead-wood and total area of stumps. This total area of dead wood was used to evaluate the numbers of seedlings growing on dead-wood per hectare. The area of other microhabitats, in which seedlings grew, was calculated as the cofactor of the dead-wood area to the whole area of permanent plots.

Densities of seedlings growing on lying dead-wood and stumps were calculated in the same way. These were categorised by dead wood origin (cutting, uprooted trees, broken trunks, and impossible to recognise) and the level of its decomposition (Table 2).

Seedling damage was analysed only for spruce and mountain ash, because other species were rare.

Generalised Linear Models with canonical link function (LEPS & ŠMILAUER 2003) were applied to test a correlation between seedling density and altitude, which was used as an explanatory variable (Table 4).

Floristic terminology follows KUBÁT et al. (2002).

	Linea	r model	Square model		
	F	р	F	р	
spruce 10–20 cm	24.47	0.000	17.40	0.000	
spruce >20 cm	3.26	0.074	1.85	0.162	
spruce ALL	9.57	0.002	4.76	0.010	
other tree species 10-20 cm	7.20	0.008	4.19	0.017	
other tree species >20 cm	11.43	0.001	11.14	0.000	
other tree species ALL	13.63	0.000	8.40	0.000	
spruce + other tree species >10 cm	12.39	0.001	6.15	0.003	

Table 4. Results of Generalised Linear Models for dependence of seedling numbers on the altitude. Results are from the permanent study plots (PSPs), significant values are in bold.

Table 5. Seedlings density recorded in the permanent study plots (PSP) of five categories; the area of each PSP was 500 m^2 .

PSP	Number	Seedling density (ind.ha ⁻¹)							
category of plots		Mean	SEM *	SD **	Median	Minimum	Maximum		
Ι	15	1,967	546	2,115	1,180	80	6,560		
II	10	3,042	808	2,555	2,270	140	7,720		
III	17	3,282	464	1,912	2,860	880	6,240		
IV	60	5,850	888	6,879	3,390	200	34,300		
V	21	6,171	1,403	6,431	4,560	640	19,580		
Total	123	4,848	522	5,793	2,960	80	34,300		

* SEM – standard error of mean; ** SD – standard deviation

RESULTS

PSPs were grouped into five categories: category I – natural gaps or opened growth historically affected by cattle grazing; category II – large scale natural disturbances (breaks and uprooted areas); category III – clear-cut areas; category IV – green tree canopy; category V – dead tree canopy.

Seedlings density in PSP of different categories is given in Table 5. The highest seedling density was recorded in plots of category V and the lowest in plots of category I, mainly located in a former grazed area on the Medvědí Hora Mt. (Judenwald). High seedling density in plots of category IV corresponded very well with the fact that more than 50% of plots were located in the first zone of the Šumava NP, where waterlogged spruce forests or other high value spruce growths occurred.

Fifty-two permanent plots were situated in an area partly managed in previous years. Trees were harvested and all or some of the economically important parts of logs were removed. Dead wood, a suitable microhabitat for regeneration, covered about 4% of these plots and only 9% of seedlings grew on dead wood.

Detail regeneration plot

The average number of young trees recorded in a DRP was 7,882 individuals per hectare. The most common species was spruce with its 7,390 ind.ha⁻¹ (Table 6).

Table 6. A comparison of the tree species regeneration recorded in 123 small regeneration plots (DRP, 28.27 m²) and 123 permanent study plots (PSP, 500 m²), densities per hectar are recalculated for either plot type (ind.ha⁻¹).

Tree species heigh	Tree species regeneration density in DRP					Tree species regeneration density in PSP				
class	Mean	SEM *	SD **	Median (ind.ha ⁻¹)	Mean (ind.ha ⁻¹)	Mean	SEM *	SD **	Median (ind.ha ⁻¹)	Mean (ind.ha ⁻¹)
spruce 10–20 cm	5.8	1.2	13.8	0.0	2,050.2	58.1	9.6	106.6	340.0	1,162.9
spruce >20 cm	15.1	2.6	28.7	1,414.7	5,339.7	161.0	19.4	214.8	1,840.0	3,219.7
spruce total	20.9	3.3	37.0	2,122.1	7,389.9	219.1	25.3	280.5	2,720.0	4,382.6
other species 10-20 cm	0.2	0.1	0.6	0.0	71.9	6.0	1.5	16.9	20.0	119.5
other species >20 cm	1.2	0.3	3.6	0.0	419.8	17.3	2.7	29.6	120.0	346.2
other species total	1.4	0.3	3.8	0.0	491.7	23.3	3.6	40.0	160.0	465.7
all species total	22.3	3.4	38.0	2,122.1	7,881.5	242.4	26.1	289.7	2,960.0	4,848.3

* SEM – standard error of mean; ** SD – standard deviation

Table 7. Seedling numbers (ind.ha⁻¹) of the different height classes; means from 123 small regeneration plots (DRP, 28.27 m²).

Height classes	0.10–0.20 m	0.21–0.40 m	0.41–0.60 m	0.61–1.00 m	1.01-1.30 m	1.31-1.50 m	>1.51 m
Norway spruce (Picea abies)	2,191	2,036	986	1,027	566	173	411
Mountain ash (Sorbus acuparia)	52	60	49	69	35	6	35
European beech (Fagus sylvatica)	14	3	9	3	3	0	3
Goat willow (Salix caprea)	9	0	6	12	0	0	0
Others	6	14	20	26	0	6	55
Total	2,272	2,113	1,070	1,136	604	184	503

Norway spruce (*Picea abies*) and mountain ash (*Sorbus aucuparia*) were the most common (93.8% and 3.9%, respectively) seedlings occurring in the DRPs. Other species were rare (*Frangula alnus* 0.6%, *Alnus glutinosa* 0.5%, *Fagus sylvatica* 0.4%, *Salix caprea* 0.3%, *Betula* sp. 0.3%, *Abies alba* <0.1%, *Acer pseudoplatanus* <0.1%, *Pinus sylvestris* <0.1%). The proportion of spruce seedlings slowly declined in the higher categories of regeneration. A small increase in the proportion of spruce seedlings compared to previous categories was recorded only in 0.61–1.00 m and >1.51 m categories. Spruce seedlings comprise 53.6% of all species regenerating in height categories 0.10–0.40 m. Many (average 3,497 ind.ha⁻¹) well-established young trees taller than 0.40 m were recorded in the DRPs. Density of mountain ash seedlings varied from 6 to 69 ind.ha⁻¹ in different height categories. An average density of more than 35 ind.ha⁻¹ was recorded in six of the seven highest categories (Table 7).

Ninety-two percent of spruce regeneration was described as natural, 1% was planted, and 7% of unknown origin. Ninety-seven percent of mountain ash was natural regeneration, less than 1% came from artificial planting, and 2% of seedlings were of unknown origin.

No damages were recorded for more than 92% of young spruce trees occurring in the DRPs (Fig. 2). In the case of damage, mechanical injuries by snow, falling trees or branches were the most common. Grazing of terminal shoots or branches was also recorded, but pee-



Fig. 2. Damages of spruce and mountain ash in damage classes: 1 - no damage, 2 - mechanical damage, 3 - terminal browsing, 4 - lateral browsing, 5 - peeling, 6 - fraying, 7 - damage to current year shoots caused by frost.

ling and browsing were uncommon. A combination of different damages on spruce trees was rarely recorded: two different damages (grazing both terminal shoots and branches) were recorded from five young spruces only and a combination of three different damages was recorded only once from a total number of 2,570 spruce seedlings.

Mountain ash seedlings were damaged more. Only 29% from 106 individuals were without visible damages (Fig. 2). Browsing of terminal shoots and branches or their combination were the most common injuries recorded. Also mechanical injuries by snow, falling trees or branches, and peeling and browsing were often recorded. Combinations of several different damages on young mountain ash trees were recorded more often than in spruce trees. A combination of two different damages was recorded nineteen times and a combination of three damages was recorded eleven times. Five young mountain ashes were injured by a combination of four damages. The combination of grazing of both terminal shoots and branches occurred most often.

The density of regeneration in different microhabitats was not equal (Fig. 3). About 80 % of regeneration was recorded from microhabitats 'litter' and 'other vegetation', which were the most common microhabitats occurring in the DRPs.

Entire permanent study plot

An average density of regeneration recorded in the PSPs was 4,848 ind.ha⁻¹. The most common species was spruce with a density of 4,383 ind.ha⁻¹ (Table 6).

There was a high variability in numbers of seedlings recorded in different plots (Figs. 1, 4). More than 500 seedlings per hectare were recorded in 93% of the plots and more than 1,000 ind.ha⁻¹ were found in 80% of the plots. The most common (29%) were plots with 1,000–3,000 ind.ha⁻¹.

There was unequal density of regeneration in different microhabitats in the PSPs. The highest proportion of natural regeneration was recorded in the microhabitat 'laying dead wood', which covered about 5.3% of the PSP area. Laying dead wood together with microhabitat 'stumps' (0.3%) covered 5.6% of the PSP area.



Fig. 3. Tree species regeneration in different microsite types: 1 - litter; 2 - other vegetation; 3 - grass turf; 4 - lying deadwood; 5 - stumps and snags; 6 - litter on stones; 7 - mineral soil.



Fig. 4. Distribution of plots by count categories of tree species regeneration in the entire permanent study plots (PSP).

If the whole PSP area was covered by deadwood, the average density of young trees growing on these dead-wood microhabitats would be 11,183 ind.ha⁻¹. If the whole PSP area was covered by other microhabitats, the average density of young trees growing on other microhabitats, which cover 94.3% of PSP area, would be only 4,473 ind.ha⁻¹. The most seed-lings were recorded on laying dead wood of decay stages 2, 3 and 4, and on stumps of decay



Fig. 5. Tree species regeneration on lying deadwood and stumps classified by the stages of decay (for stages of decay, see Table 2).



Fig. 6. Tree species regeneration on lying deadwood and stumps classified by its origin: 1 – impossible to recognize origin; 2 – cutting; 3 – uprooted; 4 – broken trunks (stumps).

stages 4 and 5 (Fig. 5). The most seedlings were recorded on broken trees, uprooted trees, and logs remaining after salvage logging (Fig. 6). Significant differences (χ -square = 3,665.651, df = 1, p<0.001) in regeneration on untreated laying trees and decorticated trees (bark was rubbed off to avoid bark-beetle infection) were recorded. More than 95% of regeneration occurred on untreated laying trees. Untreated laying trees comprised 74% of all trees in a PSP, while 26% were decorticated trees. Density of seedlings growing on untreated laying trees was 7,919 ind.ha⁻¹, while it was only 1,915 ind.ha⁻¹ on decorticated trees, i.e.,

four times less. Trees of unknown origin (most of them with high degree of decomposition) were excluded from analysis.

The dimension of laying dead wood was also found to be important. The highest proportion of seedlings was recorded on untreated laying trees with 0.21-0.30 m diameter and decorticated trees with 0.31-0.40 m diameter.

DISCUSSION

Regeneration density

The numbers of seedlings recorded from the beginning of our long-term project in the PSPs, i.e., the regeneration density, are very similar to the numbers of seedlings and young trees recorded in other surveys in both the Šumava NP and Bavarian Forest NP (PODRÁZSKÝ et al. 1999; SVOBODA 2007; VON BAUER et al. 2008; BAČE et al. 2009; HEURICH 2009). Also the high numbers of seedlings recorded in plots of categories III (clear-cut areas), IV (green tree canopy), and V (dead tree canopy) corresponded with results of other studies conducted in the same (JONÁŠOVÁ 2004) or similar forest types (BOUCHER & MEAD 2006; BOGGS et al. 2008).

HEURICH (2009) found about 5,240 young trees per hectare taller than 10 cm and 4,502 of them taller than 20 cm in mountain forests of the Bavarian Forest National Park. This was only a little bit more than our average density of 4,848 ind.ha⁻¹ (young trees taller than 10 cm). The lack of differences in species composition of the investigated plots in the Šumava NP and Bavarian Forest NP confirmed that the same biotopes occur in either NP. Norway spruce was the most common species in both study areas (90% in the Bavarian Forest NP and over 93% in the Šumava NP). There was a higher proportion of mountain ash (*Sorbus aucuparia*) in the Bavarian Forest NP than in the Šumava NP (9% vs. 3.9%, respectivelly), while several more species were recorded from the Czech plots.

In the Bavarian Forest NP, seedling numbers in the 0.10-0.20 m category were the only ones significantly lower than the numbers found for other categories (HEURICH 2009). This author found that 48% seedlings were in the height category 0.10-0.40 m and 3,000 ind.ha⁻¹ were taller than 0.40 m. This is very similar to our records of 3,497 ind.ha⁻¹ taller than 0.40 m.

Damages to natural regenerating trees were also reported from the Bavarian Forest NP. About five percent of spruces were affected by browsing of terminal shoots, while 35% of mountain ashes were grazed (HEURICH 2009).

Von BAUER et al. (2008) showed the relationship between mortality of spruce regeneration and height; mortality of regenerating seedlings rapidly decreased once the seedlings were taller than 10 cm. About 300–500 seedlings per hectare are recommended as a minimum number for maintaining mountain spruce forests (ZATLOUKAL 1999). We recorded these minimum numbers in more than 90% of the study plots. The highest number of seedlings recorded in the PSPs was 34,300 ind.ha⁻¹, while the lowest number was 80 ind.ha⁻¹. Low seedling numbers were found mainly in the Medvědí Hora Mt. (above 1,100 m a.s.l.), where the forest grazing was allowed by the so-called 'Poschinger's grazing permit' during the first half of the 19th century. Subsequently, the forest was cut down and only a few mature trees were left to produce seeds. No artificial planting was applied and the clear cut area was grazed again. An assignment of this 'forest property' to 'pasture field' was proposed during the second half of the 19th century (MINISTR 1962). Recently, an open spruce forest with many gaps occurred there. The adult trees, many of them more than 100 years old, probably naturally regenerated on stumps after clearing of the area. Blueberries (*Vaccinium myrtillus*), together with mat-grass (*Narduus stricta*) and wavy hair-grass (*Avenella flexuosa*), are the



Fig. 7. Comparison of spruce regeneration density in the small detail regeneration plots (DRP) and in the entire permanent study plots (PSP). The bold line shows the median number and the cross shows the arithmetic mean. The box encloses the first to third quartile.

most common species growing in this gap forest, which offers a high quality habitat for many species including the capercaillie (*Tetrao urogallus*), a mysterious species of mountain spruce forests.

Regeneration in entire permanent study plots vs. detail regeneration plots

Two different types of plots, PSPs and DRPs, were investigated to obtain complex knowledge about regeneration of mountain spruce forests in the Bohemian Forest.

Lower average numbers of seedlings per hectare were recorded in most PSPs vs. DRPs (cf. Table 6, Fig 7). Only in the category 'other species 10–20 cm' was a lower relative abundance of seedlings recorded in PSP compared to DRP. These results confirmed the propriety of using PSP for investigating basic characteristics (numbers and species structure of regeneration). Investigating regeneration in PSPs was very important because seedlings of natural regeneration were irregularly distributed, often clustered, and could be missed or overestimated during investigation in the small DRP only. Investigations in the small DRPs produced important additional information (e.g., origin of seedlings or their damage type) that were too labor-intensive and could only be studied in small plots.

Natural regeneration versus artificial planting

About 92% of seedlings were classified as 'natural regeneration'. This high proportion was recorded in spite of the fact that there were no significant differences in habitus of artificial-

ly planted seedlings and nature regeneration in several plots and some seedlings were recorded as seedlings of unknown origin.

To explain very often-asked questions about the origin of seedlings growing in 'non-intervention zones', we briefly analysed the history of trees planted in a part of the Modrava forest range, which is located in central part of the Šumava NP. No bark-beetle intervention management was applied in forest sectors 54, 55, 56, 74, 75, 76, 77, 80, 81, 82 (Mokrůvka and Pytlácký Roh) since 1995. Since 1994 in total, about 989,470 seedlings of spruce, mountain ash, beech, maple, and birch were planted in this area. The total area of this 'non-intervention zone' is 1,325.98 ha. The 1st zone (478.68 ha) of the Šumava NP was excluded from artificial planting, which was allowed only in the 2nd zone (847.30 ha). If the effects of self-thinning and natural mortality were excluded from the calculation, than 989,470 seedlings planted in the 847.3 ha of the 2nd zone could mean a seedling density of 1,168 ind.ha⁻¹. We found, however, that the density of seedlings taller than 20 cm was four times higher in 17 PSPs in this location (one PSP in the 1st zone and 16 PSPs in the 2nd zone of the Šumava NP). This calculation clearly showed that natural regeneration was sufficient and played a dominant role in the restoration of the mountain spruce forests after large-scale disturbances.

The importance of natural regeneration after large-scale disturbance was confirmed also from other coniferous forests (Jonášová et al. 2010). The importance and effectivity of artificial planting in similar conditions is very low. Many authors have already mentioned the benefits of natural regeneration for a progressive ecological forestry (e.g., FRANKLIN et al. 2007; SVOBODA 2007), but implementation of new knowledge to practice is very slow, even in the national park forestry.

Regeneration in different microhabitats

The importance of dead wood for successful regeneration of different tree species was studied in different geographical regions (HARMON et al. 1986; SIPPOLA et al. 1998; ZIELONKA 2006; PITTNER & SANIGA 2008). Dead wood, both laying old trees and trunks, covered only 4% of the mountain spruce forests area in the Carpathians, but 43% of seedlings occurred in this microhabitat, which was more humid than mineral soil and supported the growth of symbiotic mycorrhizal fungi (ZIELONKA 2006). We found that 1% of seedlings grew on dead wood, which covered about 5% of our study plots. The lower proportion of seedlings growing on dead wood was probably a result of the fact that some of our permanent plots were located in young uprooted areas, which were made by the windstorms Kyrill (January 2007) and Emma (March 2008). Most of the dead wood lying in these plots has not been decomposed yet and there were not many suitable microhabitats for seedlings. Seedling density was 3,042 ind.ha⁻¹ in 10 permanent plots located in young uprooted areas. Dead wood covered 15% of these plots and 17% of seedlings were growing on this microhabitat. Most of these seedlings were already growing there before the windstorms. Faster growth can be predicted now after opening of the canopy. Similar results confirming seedling occurrence before large-scale disturbances (both windstorm and bark beetle) were recorded also in the Trojmezná site at more than 1,200 m a.s.l. (BAČE et al. 2009).

The proportion of seedlings occurring on dead wood corresponded very well with the distribution of different decomposition degrees. High seedling density on dead wood of decomposition degree 2 (Table 2) corresponded with the 68% abundance of this type of dead wood. Mosses that supported seedling propagation covered most of these slowly decomposed lying trees.

Dead wood is a very important microhabitat for natural regeneration (BOBIEC 2005; ULB-RICHOVÁ et al. 2006). The quality as well as the amount of dead wood available in an ecosystem is important. Several authors described dead wood habitat qualities with different decomposition processes in different conditions (i.e., LAAKSONEN et al. 2008; LONSDALE et al. 2008). We suppose that not only different decomposition trajectories, but also pure mechanical reasons can explain the significant differences in numbers of seedlings growing on decorticated stems and untreated laying dead wood. The ruggedness of bark together with branches and knots offer more suitable sites for seed germination compared to decorticated plain stems. Similar reasons can also explain the differences in numbers of seedlings growing on laying dead wood and stubs or broken trees fragments. A recalculation of seedling number on available dead wood area showed that more seedlings grew on stubs or broken trees fragments, which offered more diverse and rugged sites. Especially broken stems often accumulate water in the broken parts which support decomposition and offer good microhabitat conditions for seedlings. Better water accumulation properties and more stable hydrological conditions can also explain our results showing that mosses are a more suitable microhabitat for seedlings than grasses, which create dense turf and compete with young trees for light and other resources (ULBRICHOVÁ et al. 2006).

CONCLUSIONS

From our results we can assume:

1) There are enough seedlings and young trees growing in mountain spruce forests in the Bohemian Forest to guarantee the natural regeneration of these habitats. More than 1,000 seedlings per hectare were recorded in 80% of the study plots and more than 500 seedlings per hectare were recorded in 90%.

2) Many seedlings and young trees, ensuring forest recovery, already occurred in plots, which were affected by large-scale disturbances (windstorm, bark beetle), before the disturbance event. This fact should be strongly reflected in all post-disturbance forest management activities.

3) Both dead wood quantity and quality (level decomposition, structure, distribution in forest, etc.) are crucial for succeful natural regeneration of mountain spruce forest. There are significant differences in the number of seedlings growing on salvaged logs and natural dead wood. Salvaged logs are a less suitable habitat for tree regeneration than decomposing dead wood.

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1991 (HEURICH et al. 2010). Repeated investigation has already found a high degree of natural regeneration with good diversity and spatial distribution. Successful recovery of mountain forests in the Bavarian Forest NP after windstorm and bark beetle outbreaks has been confirmed (HEURICH 2009).

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Abstrachicrohabitats are the most important for natural regeneration? The first results of the popping project, a long-term inventory project, which was established in non--interventionestration the Sumava National Park, a large Natura 2000 site, are published in this paper. A number ne isinameter naveral readership aremanane adata to describe the creecies replicential activities of Bohemian forest generation and the states and the second states and the states and the states and the states of the second states and the states and the states of the second states and the second states of the second states and the second states and the second states of the second states and the se over tipe and cleaner the librowin inclusive the more than of the international of the second statement of the second sec boundary in the study was been a study was been been a study of mountain spruce forests seriously affected by a the treated by the second standard and the second of the second state of the second st of the repearing time was dated in finited with a lange dated and the state of the solir the so ind.ha-Tr(median211,220000ha, and a then wall is generation platsed make have carely tebogration section and characteristics surveys clark to wat have the an unrespected in the angle of the angle of the contracteristics are averages in the order of the contracteristic averages are averages in the contracteristic averages are averages in the contracteristic averages are averages and the contracteristic averages are av spruce (breats in the Belenning Sareh shift av Chu fareh) this shanan be also in a state of the ensuring deservation of the second of the second state and the second second second second second second second on, structura distribution in interstandishare or used by the second provided of the second created fluester, salvage logener operation, 82 hile bistine stud avaster of for super estate 2001) best fewily sarres up 2001 suitabla for spire ence weithion. Wate composed that the area the and the study one of beitwood data as a part of e most post-dietythawer ifeestammeseemeestactivities in mennafi in ofests shafter palouilitanti spaloe if seests grow at altitudes

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Two national parks, the Bavarian Forest NP and the Šumava NP were established in the Bohemian Forest in 1970 and 1991, respectively. These two parks protect together 22,670 ha of mountain spruce forests, one