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Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak

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Abstract

In the 1990s, a bark beetle (*Ips typographus*) outbreak caused a dieback of semi-natural mountain spruce (*Picea abies*) forests in the Šumava National Park (Czech Republic). Two different approaches were applied to the attacked forests: (1) a small portion of the stands in the core zone of the national park was left without intervention, relying upon natural regeneration, and (2) traditional technical measures were adopted, in which attacked trees were felled and removed. Under the dead canopy of the stands left without intervention, there was a good regeneration of spruce and rowan (*Sorbus aucuparia*) and, sporadically, beech (*Fagus sylvatica*). In clear-cut areas, the numbers of spruce and rowan were significantly lower than under the dead canopy. Pioneer species such as willow (*Salix aurita*), birch (*Betula pubescens*), and aspen (*Populus tremula*) appeared in the clear-cut areas. The dependence of spruce regeneration on the availability of suitable microhabitats was found: decaying wood and spruce litter was found as the most favourable. The results confirmed that the original tree species of the mountain spruce forests regenerate well under dead canopy. The bark beetle outbreak does not result in the complete loss of the forests and could even be considered as a tool for the restoration of their natural character. © 2004 Elsevier B.V. All rights reserved.

Keywords: Bark beetle outbreak; Decaying wood; Forest management; Mountain spruce forest; Natural regeneration; Picea abies (L.) Karst

1. Introduction

The bark beetle *Ips typographus* (L.) and some other bark beetle species are integral parts of any natural Nor-

* Corresponding author. Tel.: +420 387 772 220; fax: +420 385 310 366. way spruce (*Picea abies* (L.) Karst.) forest by maintaining the dynamics of forest development. The beetles act as factors selecting against less vital, overmatured, somehow disadvantaged, and, under natural conditions, less adapted individuals, which succumb to their attack mole easily (e.g. Barbosa and Wagner, 1989; Berryman, 1986; Byers, 1996; Jakus, 1998; Tunset et al., 1993). By creating space for a new genera-

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tion of spruce, they make the natural regeneration of the forest possible. However, forests influenced and changed by anthropogenic factors are more susceptible to bark beetle attacks, so bark beetles are usually considered to be very dangerous pests in every forest except for strictly natural virgin forests. This situation often leads to controversies about management interventions against bark beetle in protected areas and national parks, which are a mosaic of strictly natural and human-influenced forests.

The problem of large-scale bark beetle outbreaks is of interest for all of Central Europe, where spruce forests are original in mountainous areas and the planting of spruce in cultures has a long tradition. Mountain spruce forest dieback, connected with bark beetle outbreaks, has affected most mountains of Central Europe. There are many possible causes for this situation. The cumulative impact of several alterations to the environment, including global climate change, air pollution, and the long-term influence of preferring spruce by forest managers resulted in changes in nutrient cycling, litter accumulation, and soil acidification. This process was described by Fanta (1997) and Emmer et al. (1998, 2000) as the process of "anthropogenic borealisation", with reference to the boreal spruce forest zone. The injured stands die from bark beetle attack much easier resulting in a rapid, large-scale degradation of the spruce forests, similar to the degradation phase of boreal spruce forests (Fanta, 1997).

The problem for managers lies in deciding in which stands the bark beetle can be considered to be a natural part of forest dynamics, and in which it is a pest. Not long time ago, it was thought that declining spruce forests were not able to regenerate sufficiently after massive bark beetle outbreaks. Thus, bark beetle occurrence was strictly suppressed everywhere, even in national parks, with only rare exceptions in the case of a few, usually small, well-preserved virgin forest reserves. The first break from traditional forest management occured in the Bayerischer Wald National Park in Germany. An extensive area of the core zone was left without any active management intervention after extensive wind throws in 1983 and 1984 and following bark beetle outbreaks (Bibelriether, 1991; Bibelriether et al., 1995; Kiener, 1990; Strunz, 1994). Results from research on the development of such affected forest were presented by Fischer et al. (1990), Fischer (1992), Heurich (2001), Huber (2000), Jehl (2001), Mosandl and Fischer (1999), and Nüßlein and Faißt (1998). The non-intervention approach is often being applied now in many protected areas of European forests, at least in a portion of these areas (e.g., Broekmeyer and Vos, 1993; Bücking, 1997; Hullen et al., 1994; Stöcker, 1997). A common question in regards to this passive management regime is how large area of forest can be left without any intervention.

This is the case in the Šumava National Park. The forests in this park were affected by a massive bark beetle outbreak in the 1990s, especially the extensive mountain spruce forests in the central part of the mountains, which were partly changed and influenced by forest management in the past. Massive bark beetle outbreaks have been documented in the Šumava Mts. since the 19th century (Jelínek, 1988). Besides remnants of the original natural forests, there are many semi-natural and planted spruce stands. Only the stands supposed to be natural and uninfluenced were left as small reserves, and active interventions against bark beetle were applied in the other stands. Managed and unmanaged stands are scattered in a mosaic, together with valuable peat bogs and waterlogged forests; thus, interventions in the form of cutting affect the whole area.

The objectives of this study were: (1) to compare the establishment and survival of tree species in dead spruce forests and in clear-cuts which originated from interventions by foresters, and (2) to find out the best strategy for forest regeneration in the affected areas.

2. Study area

Permanent research plots were located in the central part of the Šumava Mountains in the area of Březník, approximately in the area between the peaks Lusen and Rachel on the Czech side of the border with Germany (48°56′–48°59′N, 13°25′–13°29′E, Fig. 1). The altitude ranged between 1175 and 1280 m above see level. The climate is cool and wet, with mean annual precipitation about 1500 mm and mean annual temperature about 4 °C. The bedrock is predominantly gneiss, partly combined with granodiorites. Mountain humus podzol, with a thick layer of raw humus and a leached eluvial horizon, is the prevailing soil type. Gley soil and peaty soil occur in depressions (Chábera, 1987).

The forests in the studied area can be included in the alliance *Piceion excelsae* Pawlowski in Pawlowski,



Fig. 1. The location of the study area within the Czech Republic and within Europe.

Sokolowski in Wallish 1928. The unit includes acidophilous climax mountain spruce forests and edaphically conditioned waterlogged spruce forests. The tree layer is dominated by Norway spruce (P. abies), often together with rowan (Sorbus aucuparia). European beech (Fagus sylvatica), silver fir (Abies alba) or pubescent birch (Betula pubescens) can be admixed. Norway spruce forms relatively closed stands, except on peat bogs where they are rather open. Acidophilous herbs and dwarf shrubs including villous smallreed (Calamagrostis villosa), wavy hair-grass (Deschampsia flexuosa), and Vaccinium spec. div. are dominant in the herb layer. Purple colt's-foot (Homogyne alpine), chickweed-wintergreen (Trientalis europaea), great wood-rush (Luzula sylvatica), and broad buckler-fern (Dryopteris dilatata) are also frequently present. The moss layer is usually dominated by Polytrichum formosum or Dicranum scoparium in drier sites, and it is especially well-developed in waterlogged sites, typically with Sphagnum sp. div. as a dominant (Moravec et al., 2002).

The first impacts from logging, without serious influence on the forests, were reported from the 17th century. The first important interventions, significantly influencing and changing the forests in the studied area, started at the beginning of the 19th century (Pišta, 1972). Spruce monocultures which were planted after cutting, wind throws and bark beetle outbreaks, prevail now on sites of former climax spruce forests. These

stands have a rather homogenous structure with rowan being the only broadleaved species present, although one would expect at least a small admixture of beech in the tree layer (Neuhäuslová, 2001). The rowan grows on the forest margins and colonizes temporarily openings in the spruce canopy. The most valuable and preserved stands, the least influenced by humans, are the edaphically conditioned waterlogged and peat bog spruce forests.

3. Methods

3.1. Research plots

Eighteen 400 m^2 permanent research plots were established in representative parts of the available stands. The plots were chosen to represent stands with and without interventions against the bark beetle. The stands are described as follows:

- 1. Dead canopy, i.e. climax mountain spruce forest, which was attacked by bark beetle and died in 1996 and 1997, left without interventions, the canopy cover was reduced on average from 41% in 1997 to 11.5% in 2002 due to the natural falling of parts of dead trees (eight plots),
- Clear-cut climax mountain spruce forest, which was attacked by bark beetle and completely cut down in 1997 (five plots),
- 3. Waterlogged spruce forest—attacked by bark beetle in 1998, partly survived (about 20% of trees in the tree layer), the canopy cover was reduced on average from 50% in 1997 to 28% in 2002 (five plots).

There was only spruce in the tree layer of all of the investigated stands, and their structure was rather homogenous. The herb layer consisted of all the typical species of climax mountain, respectively, waterlogged spruce forests (see above).

3.2. Amount of natural regeneration

Natural regeneration was measured by recording annually the numbers of seedlings of all tree species from 1997 to 2002, except in the waterlogged forests which were monitored from 1998 to 2002. All seedlings were recorded and divided into two height categories: (1) \leq 50 cm, (2) >50 cm. Spruce seedlings were divided also into age-categories: (I) 1-5, (II) 6-10, (III) 11-20, (IV) >20 years, based on counting of the whorls.

3.3. Microhabitat preferences of seedlings

The relationship between the regeneration of particular species and various microhabitats was evaluated from 1998 to 2002. Whether this relationship differed between plot types and over time was also analyzed. Microhabitats analyzed included patches of particular herb species, decaying wood, mosses, and spruce litter. The decaying wood microhabitat was defined as stumps and laying logs of various decay rate. The laying decaying logs overgrown by herbs or mosses which were still well-distinguishable, were also considered as the category of decaying wood. The type of microhabitat where the seedlings were found was recorded for each tree species. Seedling numbers were related to the extent of each microhabitat and their densities in particular microhabitats were calculated. The extent of each microhabitat was determined by visually estimating its percentage in each plot. In the case of spruce, only the youngest age-category of seedlings, which originated in the mast year 1995, was evaluated. This group of seedlings was the most numerous and was easily distinguishable from older seedlings. From these data, we were able to determine the most favourable microhabitat both for the germination and survival of spruce seedlings.

3.4. Statistics

Differences in seedling numbers in the different types of plots and in different years were evaluated by redundancy analysis (RDA) using the Canoco programme (Ter Braak and Šmilauer, 1998). Time was considered to be a quantitative variable. Plot types interacted with time were used as explanatory (environmental) variables and seedling numbers of particular tree species as response (species) data. Seedling numbers were logarithmically transformed: ln(1 + seedling number). A Monte Carlo permutation test with split-plot design was used to test for significance, the records done in different years in the same plot were subplots of the same main plot and only the main plots were permuted. The criteria for those explanatory variables to be included in the model were set to $P \leq$ 0.05. The resulting ordination diagrams were produced by the CanoDraw programme (Ter Braak and Šmilauer, 1998).

Differences in seedling numbers (respectively densities) among microhabitats, and extent of microhabitats over time and plot type were tested by repeated measurement ANOVA (Statistica 6.0 programme).

4. Results

4.1. Amount of natural regeneration

Seedlings of six tree species were found. Average numbers of spontaneously occurring seedlings for particular species in each year and plot type are presented in Fig. 2a-c. The seedlings of all the species divided into the height categories in observed three types of plots in relation to the time are shown in Fig. 3 where results of RDA analysis are presented. The Monte Carlo permutation test proved the significant influence of the type of plot in interaction with time on numbers of seedlings (F = 11.43, P = 0.001). This means that species development and height composition during the study period was dependent on plot type. There is an obvious difference between the two types of stands, i.e. waterlogged forests and dead canopy on one side, and clear-cuts on the other side. The typical species of clearings, such as birch (Betula pubescens), willow (Salix aurita) and aspen (Populus tremula), significantly preferred clear-cuts, while beech (Fagus sylvatica), a species of climax mountain forests, was found only in the dead canopy stands and rarely in the waterlogged forest. A more complicated situation occurred with spruce and rowan (Sorbus aucuparia), which were the most numerous regenerating species. Rowan was significantly the most successful under the dead canopy, although seedlings less than 50 cm in height were also found frequently in the waterlogged forests. Rowan seedlings taller than 50 cm were significantly positively correlated with the dead canopy. The total numbers increased during the study period, especially under the dead canopy, where the highest numbers were found (between 100 and 600 seedlings/ha in 2002). In contrast, rowan numbers ranged between 50 and 175 seedlings/ha in 2002 in the clear-cuts and were lowest in the waterlogged forests (0-100 seedlings/ha in 2002), even slightly decreasing during the study period.



Fig. 2. (a-c) Average numbers of seedlings of the particular species per hectare in each year of observation in three types of plots.



Fig. 3. Relationship between numbers of seedlings and type of plot in interaction with time (RDA analysis, F = 11.43, P = 0.001). Seedlings were classified into height categories: Spruce1, Rowan1, Beech1, Aspen1, Birch1, Willow1—seedlings \leq 50 cm; Spruce2, Rowan2, Aspen2, Birch2, Willow2—seedlings >50 cm.

Spruce formed the main part of natural regeneration in all of the plots during the whole study period, but its height and number differed between the plots. Seedlings less than 50 cm were found preferably in the waterlogged forests, where a slight positive trend in their numbers was found, evidently due to the surviving fertile trees. However, their numbers decreased under the dead canopy and in the clear-cut plots. Seedlings taller than 50 cm increased in number over time both under the dead canopy and in the clear-cuts, and they stagnated in the waterlogged forests.

There were also large differences among the plot types when analyzing spruce regeneration based on age classification (Fig. 4). As with the size classes, there were significant plot type with time interactions (Monte Carlo permutation test: F = 22.62, P = 0.001), which means that the temporal trend in age composition of spruce regeneration was dependent on type plot. The largest part of spruce regeneration was formed by the

youngest seedlings (age-category Spruce I). But their numbers decreased over time, especially in the clearcuts, whereas in the waterlogged forests they increased slightly. All of the other age-categories were most numerous under the dead canopy, where a natural-looking age structure was present, with many young seedlings and lower numbers of older seedlings. The numbers of the older seedlings also increased in the clear-cuts, but not so much as under the dead canopy. The opposite situation was found in the waterlogged forest, where the older age-categories were rare and their numbers decreased during the study period.

Total spruce seedlings numbers slightly decreased in all plot types due to a natural decrease of the youngest seedlings which germinated in several mast years in the 1990s. Seedlings of the other deciduous species mostly increased in numbers, from a proportion of about 0.7% of all seedlings in all plot types in 1997, to almost 5% under the dead canopy, 4% in the waterlogged forests, and 10% in the clear-cuts by 2002.



Fig. 4. Relationship between numbers of spruce seedlings and plot type in interaction with time (RDA analysis, F = 22.62, P = 0.001). The seedlings were classified into age-categories. Spruce I < 5, Spruce II 6 – 10, Spruce III 11 – 20, Spruce IV >20 years old seedlings.

4.2. Microhabitat preferences of seedlings

The microhabitat preferences were found only in the case of spruce seedlings; regeneration of broadleaved species was found not to be dependent on the type of microhabitat. The total numbers of spruce seedlings differed significantly between the different types of microhabitats (Fig. 5a) both within plot type (interaction microhabitat \times plot type F = 2.871, P < 0.005) and over time (interaction microhabitat \times time F = 20.536, $P < 10^{-6}$). At the beginning of the study period, most seedlings were found in three types of microhabitats (decaying wood, spruce litter and mosses) in all of the plots. The proportion of the seedlings along with the total number of seedlings and their survival changed in particular microhabitats over the study period. Under the dead canopy, most of the seedlings grew in the spruce litter even after a large decrease in their numbers, while by 2000 most seedlings were found in the decaying wood in the clear-cut and waterlogged forest plots. The fastest decrease of seedling numbers in the spruce litter was observed in the clear-cut plots (Fig. 5a): the fewest numbers of seedlings were found in this microhabitat in 2002.

Significantly lower numbers of seedlings were found in the stands of the herb species Vaccinium myrtillus, Deschampsia flexuosa and Calamagrostis villosa. In other types of vegetation (Lycopodium annotinum, Oxalis acetosella, Dryopteris dilatata), seedlings were found only very rarely and these microhabitats were not included in the statistical analysis. Nevertheless, seedling numbers were increasing gradually in the herb vegetation in all of the plot types, just as their original microhabitats (spruce litter, mosses) were being replaced by herb vegetation.

To find out the most important microhabitats for regeneration, seedling densities (seedling number/ 100 m^2) were calculated for each type of microhabitat (Fig. 5b). The densities of seedlings in the microhabitats differed significantly in the three plot types (F = 3.665, P < 0.0007) and in the plot by time interaction (F = 11.775, $P < 10^{-6}$). Decaying wood was the most favourable microhabitat both in clear-cuts and in waterlogged forests. Higher densities of seedlings were found in spruce litter only under dead canopy. Mosses were the third most favourable microhabitat in all plot types. Herb vegetation (the grasses *C. villosa* and *D. flexuosa*) was least favourable microhabitat, especially for the youngest seedlings. Seedling densities were



Fig. 5. (a and b) Total numbers of spruce seedlings in the experimental plots of 400 m^2 (a) and in 100 m^2 of the respective microhabitats (b).



Fig. 6. Changes in covers of the particular microhabitats during the period of observation.

increasing in *D. flexuosa* patches over time, meaning that older seedlings were able to survive in it.

The changes in the extent of the important microhabitats in each plot type during the study period are shown in Fig. 6. The repeated measurement ANOVA (the interaction between microhabitat extent, plot type and time was tested) proved a different development of the microhabitats extent in the three types of plots $(F = 6.09, P < 10^{-6})$. The herb vegetation increased in all plot types after opening or cutting of the canopy because of the bark beetle outbreak; the coverage of favourable microhabitats (mosses and litter) strongly decreased, being overgrown by the herb vegetation. Interestingly, the coverage of the whole herb layer, which is unfavorable for spruce seedlings, started to decrease since 2000 in the dead canopy stands, probably due to increased tree fall of dead trees. On the other hand, the cover of the competitive grasses continuously increased in the clear-cut stands, while litter decreased dramatically, thus decreasing the probability of the establishment of woody species. Coverage of the particular microhabitats remained relatively stable in the waterlogged forests.

5. Discussion

5.1. Amount of natural regeneration

The results showed that in comparison with clearcuts the presence of dead canopy has a significant positive effect on the regeneration of all woody species typical for climax spruce forests, i.e. spruce, rowan and beech. Differences in species composition, increasing over the course of the study, showed that development under the dead canopy will probably lead to a mountain forest with a natural species composition much sooner than development in clear-cuts. Only species of climax spruce forests were found under the dead canopy, while some pioneer and ruderal species appeared in clear-cuts. The numbers of spruce seedlings were sufficient for forest regeneration not only under the dead canopy, but also in the clear-cuts. According to Mayer and Ott (1991) at least 200 seedlings per hectare are necessary for maintaining the structure of a spruce stand. The height and age structure of regenerating spruce seedlings differed greatly between the dead canopy and clear-cut plots. The proportion of seedlings in the height categories indicates continuous growth under the dead canopy. Spruce was present in all of the age and height categories in all of the studied plots with the greatest numbers in the youngest seedling class. Nevertheless, the number of seedlings in the older and taller seedling categories started to increase vigorously under the dead canopy; it appeared that the dead canopy stimulated the successful regeneration of spruce apparently due to better light conditions. Though young spruce seedlings are able to survive in shade, they need more light to start growing; moreover, seedlings need more light under unfavourable site conditions (Ammer, 1998).

The situation is different in the clear-cut plots. Although there is enough light, the results show that the conditions are less favourable for regeneration. In the clear-cuts, the numbers of both spruce and rowan were lower than under the dead canopy, and moreover, their height and age structure was reduced. Almost all of the spruce seedlings in the youngest age category, originally the most numerous, were destroyed by cutting interventions against bark beetle or died soon after cutting due to the severe change of conditions. Also the oldest surviving seedlings were less numerous than under the dead canopy. Nüßlein and Faißt (1998) also found successful regeneration under the dead canopy in the Bayerischer Wald National Park. Regeneration was better than in intact stands due to better light conditions in stands covered with dead spruce canopy.

As a pioneer light-demanding species, rowan theoretically should have more favourable conditions in clear-cuts. Nevertheless, it also regenerated better under the dead canopy. It seems that the dead canopy has several advantages: it is open enough, thus rowan has enough light for its growth, and fallen trees provide protection against browsing by game. Browsing has been a common problem in this region and certainly reduces the establishment of rowan in the whole area (Matějková and Jonášová, 2003). However, areas with fallen trees in the Bayerischer Wald significantly reduced browsing of rowan under dead canopy (Heurich, 2001). Further, the numbers of rowan in our plots increased much more under the dead canopy during the five years of our study, whereas their numbers in clearcuts increased only slightly. This may be explained by the spreading strategy of rowan by birds, which empty their intestines after having flown some distance from seed trees (Leder, 1997) and prefer to stay in tree stands. Kollmann (1994) showed that the introduction of diaspores by birds is very rare into treeless sites. The similar probably applies to the beech in our case. There were no seed trees of beech in the areas surrounding the plots, but some new seedlings were found under the dead canopy and rarely in the waterlogged forest. Beech is capable of being spread over long distances, but as a late climax species it does not usually appear in treeless sites (e.g. Evans, 1988; Leder and Wagner, 1996). Because it can grow even in herb vegetation and does not need any special microhabitat for regeneration like spruce (Szewczyk and Szwagrzyk, 1996), beech may be expected to continue spreading into dead forests.

An interesting phenomenon is the appearance of small numbers of new spruce seedlings under the dead canopy, evidently spreading from surviving trees. Norway spruce seeds are found mostly within 50 m of seed trees (Schmidt-Vogt, 1986–1990), so it would be expected that only a lower number of new spruce seedlings would be found in the extensive dead stands where tree survivorship was only 1–5%. Nevertheless, these seedlings can be very important, because they represent the new generation of resistant spruce, which can potentially form a new forest that will be better adapted to bark beetle outbreaks (Kaňák, 1988, 1998).

In the clear-cuts, a slight increase in the number of pioneer species was apparent, although willow numbers decreased by the end of the study. All pioneer species had established by 1998, when the surface was still disturbed and there was less vegetation due to the cutting performed in 1997. After the closing of the herb layer, the number of woody species would not be expected to increase because of competition from the herb layer, and the lack of decaying wood in comparison with the dead stands.

The waterlogged spruce forests represent a special case (Neuhäuslová, 2001; Sofron, 1981). Regeneration in this plot type seems to be different compared to

the other stands. The numbers of the youngest spruce seedlings were very high; they germinated very well, being quite abundant in the moss microhabitat, but their survival and growth were low probably due to less favourable site conditions. A similar situation was reported from boreal peat and swamp forests (Hornberg et al., 1997; Ohlson and Zackrisson, 1992).

5.2. Microhabitat preferences of seedlings

The results confirmed the importance of favourable microhabitats for natural regeneration of spruce. Definitely the most favourable microhabitats for spruce seedlings were decaying wood and spruce litter. Although decaying wood covered only a small percentage of the soil surface, it harboured the largest portion of seedlings. It was the most favourable microhabitat both in the clear-cuts and waterlogged forests and the second most important after litter itself under the dead canopy. The importance of decaying wood for spruce regeneration, especially under harsh environmental conditions, has been reported from mountain spruce forests (Reif and Przybilla, 1998), from boreal spruce forests (Hofgaard, 1993; Hornberg et al., 1997; Szewczyk and Szwagrzyk, 1996) and other coniferous forests, for example, Picea sitchensis (Bong.) Carriere and Tsuga heterophylla (Raf.) Sarg. forests (McKee et al., 1982; Harmon and Franklin, 1989). Decaying logs maintain favourable temperature and moisture conditions, and protect seedlings against competition from the herb layer (Ponge et al., 1998). Reif and Przybilla (1998) described rapid spruce regeneration in dead spruce forests in the Bayerischer Wald. These forests were known for low seedling regeneration in the past, caused by a lack of decaying wood due to forest management and wood use. The situation improved rapidly after the forests were left without management; an increasing amount of decayed material and diameter of the laying decaying logs were found to be most important for regeneration. Spruce litter seems to be especially important for spruce regeneration under dead canopy. Litter may be built up by gradual tree fall together with deposition of bark and small parts of branches so that the litter is only slowly overgrown by vegetation. This "mulch" effect was observed also by Heurich (2001). Moreover, shade produced by the dead trees reduces dessication compared to the clear-cuts. Reif and Przybilla (1998) found that there were two to three times more seedlings in the spruce litter under dead canopy than under live canopy, however, the greatest portion of seedlings grew under the dead canopy on decaying wood, increasing with the diameter of logs and higher decay rate. The fact that in our investigation there were more seedlings in the spruce litter than on the decaying wood could be caused by the small diameter of decaying wood in the plots or by its insufficient rate of decay.

Mosses were the other favourable microhabitat. It was a common microhabitat with high seedlings germination. However, seedling survivorship in mosses was low, which could be caused by the fact that the cover of mosses decreased during the study.

There were no observed microhabitat preferences for broadleaves, although willows appeared in the clear-cuts only in the first years shortly after cutting, before the herb vegetation expanded. Thus, it could be assumed that they need a disturbed soil surface for germination (Nebe, 1994). The fact that we did not find any significantly important microhabitat in this case could also be caused by fast growth of the vegetation so that the willow seedlings recorded in summer were already found in the vegetation. Heurich (2001) found spruce bark and litter as the most favourable microhabitat for rowan regeneration. This microhabitat is usually found close to stems, so the frequent occurrence of rowan seedlings could be related to the way rowans are dispersed by birds. Nevertheless, we did not find any type of microhabitat that was significantly more favourable for rowan regeneration than others.

6. Conclusions

Five years after the bark beetle outbreak, it is obvious that regeneration processes under the dead canopy proceed quite well. There is enough regeneration of spruce and rowan. Beech exhibits an increasing trend after the canopy has died. Newly appeared beech seedlings, although in small numbers, can indicate a certain ability of the forests to transform themselves to a more natural species composition without human interventions. Homogeneous spruce stands, with a lack of decaying wood due to past forest management, seem to be changing due to the bark beetle outbreak to more open stands with a high amount of dead wood and an increasing proportion of indigenous broadleaved species, i.e. rowan and beech. Thus, the bark beetle should be considered as a natural tool for restoration of a natural character of the mountain spruce forests which were altered by human activities in the past.

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