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**Natural Regeneration
and Vegetation Changes
in Disturbed Norway Spruce
Forests**

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PhD. Thesis

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Annotation

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Disturbances are natural components of natural spruce forests life cycle. However, most Central-European mountain spruce forests, damaged by air pollution and influenced by forest management, are more susceptible to large bark beetle disturbances. The resulting areas of standing dead forests raised doubts about the possibility of their restoration. The results of this thesis demonstrate ongoing regeneration processes in the forests affected by bark beetle outbreak and left without interventions. In comparison to natural disturbance, the artificial disturbance resulting from interventions against bark beetle appears to be more interfering. Thus, the non-intervention strategy seems to be the best option for restoration of disturbed mountain spruce forests. Artificial disturbances in the form of forest management measures can be recommended only in man-made coniferous plantations to support natural regeneration of indigenous broadleaved species.

Declaration

I hereby declare that this thesis has been fully worked out by myself and the named co-authors with the use of cited references.

Magda Jonášová



České Budějovice, 13th November 2006

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Chapter I

General introduction

The first part of the book is devoted to a general introduction to the study of the morphology of the... This part is divided into several chapters, each dealing with a different aspect of the morphology of the... The first chapter, 'General introduction', provides a brief overview of the field and its history. The subsequent chapters, 'Study of the morphology of the...', 'Study of the morphology of the...', 'Study of the morphology of the...', 'Study of the morphology of the...', and 'Study of the morphology of the...', each focus on a specific aspect of the morphology of the... The final chapter, 'Study of the morphology of the...', provides a summary of the findings and discusses their implications for the study of the morphology of the... The book is written in a clear and concise style, making it accessible to a wide range of readers. It is a valuable resource for anyone interested in the morphology of the... and is highly recommended for students and researchers alike.

General introduction

Norway spruce (*Picea abies* (L.) Karst.) is the most common tree species in Central Europe due to extensive planting. This large scale planting has led to many problems. Transformation of these coniferous plantations to mixed stands represents one of the most important objectives of forest management in Europe (e.g. Kenk and Guehne, 2001; Spiecker et al., 2004). Natural spruce forests are, however, rather rare and of small-scale in Central Europe (Ellenberg, 1988). Moreover, large areas of natural Central European spruce forests were damaged by atmospheric pollution in the 1970's and 80's, with large parts of relatively natural spruce forests influenced by forest management. Both mountain spruce forests damaged by many anthropogenic stresses and disturbances and artificial spruce plantations can be considered as disturbed forest ecosystems (Fanta, 1997). In the strict sense of the word, natural disturbances such as wind or bark beetle outbreaks should be distinguished from anthropogenic ones, represented predominantly by cutting. Both types of disturbances can interact so that human-disturbed forests are more susceptible to natural disturbances, which normally play an important role in forest dynamics. Natural disturbances seem to occur more often and have larger impacts on forests nowadays than in the past (Schelhaas et al., 2003). Examples of this are large wind and bark beetle disturbances, which occurred simultaneously in the 1990's in Europe (Lässig and Schönenberger, 2000). Given the long-term tradition of spruce planting, the conservatism of most foresters, and the lack of information about the dynamics of natural spruce forests in Central Europe, many questions and discrepancies appear concerning approaches to natural processes in spruce forests and to the role of natural disturbances in their regeneration. Nevertheless, in respect to sustainable management and biodiversity maintenance, the contemporary trend in forestry includes simulation of natural processes in forest management and their large-scale protection in forest wilderness areas (Peterken, 1999; Parviainen et al., 2000). If the objective of spruce forest restoration is to be achieved, natural processes should be understood and widely applied.

Links between disturbances and forest regeneration (with the focus on Central-European mountain spruce forests).

Natural disturbances represent the key factor in natural forest dynamics (e.g. Bonan and Shugart, 1989; Pontaville et al., 1997). Whereas small-scale gap disturbances in the form of the death of single trees or groups of trees are common in temperate deciduous forests (Bormann and Likens, 1979), large-scale disturbances, such as fire, wind and insects, influence forest succession in large areas of boreal coniferous forests (Goodman and Hungate, 2006). Disturbances can also act together: tree death due to bark beetles is often followed by fire in boreal forests, while wind-thrown areas of mountain spruce forests are followed by bark beetle outbreaks. Disturbances influence species diversity, nutrient cycling, vegetation patterns, and are also needed for natural regeneration of many tree species. It can be used for forest management, which, by simulating natural disturbance regimes, have less impact on the biodiversity of exploited forests (Attiwill, 1994; Fries et al., 1997; Hanssen, 2003; Schmiegelow et al., 2006).

It is clear that both biotic and abiotic disturbances are natural components of virgin Central European spruce forests life cycle (Korpel, 1993; Holeksa, 1998). Natural spruce forests tend to form a uniform structure (although all-aged), which is sensitive to catastrophic destruction of the tree layer by disturbances. At least partial release of canopy closure is necessary for natural regeneration of spruce. Although saplings are able to establish and survive for decades in the shade of the parent stand, with almost negligible increment, it needs open canopy to start growing. The regeneration phase can last for one hundred years (Korpel, 1997) and is characterized by large amounts of dead wood (coarse woody debris). Dead wood represents a specific condition for spruce regeneration. It was recognized as one of the most favorable microhabitats for germination and successful survival and growth of spruce seedlings, which are not able to survive under competition from abundant grass vegetation (Hofgaard, 1993). The importance of dead wood for spruce regeneration is especially considerable under harsh climatic conditions at high altitudes (Svoboda, 2005). The presence of dead wood is the main indicator of unmanaged forests, which have a much higher proportion of both standing and laying dead wood comparing to managed ones (Bretz Guby and Dobbertin, 1996). Both essential conditions for spruce regeneration, open canopy and sufficiency of dead wood, occur as a result of natural disturbances.

In Central Europe, the first data about the natural development of spruce forests after large-scale natural disturbances were gathered from the Bayerischer

Wald National Park, where large areas of near-natural spruce forests were affected by a windstorm in 1983. The forests in the reservation zone of the park were left without any interventions, and natural regeneration and vegetation succession of blown-over forests were monitored in permanent plots (Fischer et al., 1990; Jehl, 2001). These authors found the renewed tree layer had the same composition as the previous forest, with little change in ground vegetation. The disturbance caused by bark beetle attack seems to be partially specific. Generally, it is assumed that, under natural conditions, bark beetle acts as a factor selecting against less vital, overmatured, somehow disadvantaged, and less adapted individuals (e.g. Berryman, 1986; Barbosa and Wagner, 1989; Tunset et al., 1993; Jakus, 1998). Nevertheless, in consequence of the cumulative impact of several alterations to the environment, including global climate change, air pollution, and the long-term influence of forest management, mountain spruce forests have declined in most mountains of Central Europe. Such injured stands are more affected by bark beetle attack, resulting in rapid, large-scale mortality of spruce forests, similar to the degradation phase of boreal spruce forests (Fanta, 1997). Such large areas of standing dead forests had not commonly occurred earlier in Central Europe, raising many questions and doubts about the possibility of their restoration. There are some differences in bark beetle affected areas compared to disturbances caused by wind or fire. Dead tree canopy can partly substitute the function of the previous living canopy for some time, since the trees remain standing and only gradually their parts break and fall down. The change of light conditions is gradual and there is almost no mechanical destruction of understory at the beginning, which can be crucial for the survival of tree seedlings and sensitive forest species. Nitrogen availability may increase following bark beetle outbreaks because of increased litter fall and lower nitrogen uptake via tree mortality (Lerdau, 1996).

The first studies of the natural development of Central European mountain spruce forests after bark beetle outbreak were also conducted in Bayerischer Wald and indicated only few changes in understory vegetation composition over a few years after the outbreak (Heurich, 2001; Bauer, 2002). Spruce and rowan were the dominant species in natural regeneration three years after death of the original tree layer, which indicates no pioneer phase in forest succession after bark beetle outbreak (Bauer, 2002). Nevertheless, continuing long-term monitoring is still needed.

Natural vs. anthropogenic disturbances

In many regions, natural disturbances have been mostly eliminated and replaced by forest management (Linder et al., 1997; Östlund et al., 1997). Noss et al. (2006) denote that naturally disturbed, unsalvaged forests are more rare and imperiled than old-growth forests. Management suppressing natural disturbances is also common in most natural Central European mountain spruce forests. Salvage logging, i.e. felling and removing infested stands, is still a common measure applied in forests attacked by bark beetle even in some protected areas and its impacts should be known in comparison with impacts of natural disturbances. Lindenmayer and Noss (2006) review the literature on impacts of post-disturbance logging worldwide. They conclude that the effects of salvage logging are generally different from those of logging in forests not affected by a disturbance and that forest ecosystems may be more strongly affected by post-disturbance logging than the initial disturbance. The authors mention the example of salvage logging decreasing the natural regeneration of coniferous species, which are abundant after natural disturbance. On the other hand, natural disturbances restored structures and biodiversity lacking due to forest management. Similar conclusions were drawn by Foster and Orwig (2006), who contrasted ecological effects of windstorms, invasive pests and pathogens with the impacts of salvage logging. They also found no indication that active or preemptive management improved the resistance or resilience of forests.

Natural succession in cleared and uncleared windthrow areas of mountain spruce forests in Central Europe was compared in the Bayerischer Wald (Fischer et al., 1990; Fischer, 1992). The authors found that strong soil disturbance caused by logging operations was important for the spread of pioneer species. Natural regeneration of spruce and forest herb species survived better in uncleared areas, where almost no soil disturbance occurred.

There are few comparisons between the effects of bark beetle outbreak and anthropogenic disturbance as a result of various forms of interventions against bark beetle spreading. The effects of these interventions were mostly neglected as indirect effects of bark beetle outbreak. The strongest effect can be expected in the case of classical salvage logging, when all trees in the infested stands are cut down and logged (Wermelinger, 2004). This logging is often more intense, and creates large clear-cut areas, compared to logging within regular management. A lower impact could be assumed when infested trees are cut down, debarked, and

left on the site. This approach was rarely used in Šumava National Park, with inconsistent results (see Chapter III).

Using natural processes in restoration of spruce plantations

Spruce plantations represent large-scale homogenous stands occurring often in sites outside of the natural spruce range. Their biodiversity is much lower than that of natural forests, and are relatively unstable and require a lot of additional energy in the form of various forestry measures (Carnus et al., 2006). Spruce is able to influence its environment due the formation of acidic humus, deterioration of soil structure, and changing vegetation composition to lower species diversity (Emmer et al., 1998). Their transformation to irregular and mixed stands represents a challenge for current forestry management. Nowadays, the aim is to incorporate natural processes into forest management (Mattsson, 1994). Natural processes are preferred over purely technical measures in the transformation of plantations (Fries et al., 1997; Peterken, 1999). It is likely that some natural processes that occur in natural spruce forests also function in artificial stands. Natural regeneration seems to be an effective method to transform plantations. Because natural spruce forest regeneration depends on disturbances to reduce the dense canopy (Drobyshev, 1999), knowledge of gap dynamics and, consequently, gap creation can simulate natural processes and create conditions for natural regeneration of various tree species (Diaci, 2002). Natural regeneration can be successfully used in transforming plantations from uniform to irregular stands of the same species composition (Malcolm et al., 2001; Quine, 2001). Using natural regeneration for transformation to mixed stands seems to be more complicated compared to using it only for transformation of stand structure. This depends not only on favorable site conditions, which can be influenced by canopy change, but is related to the abundances of indigenous species in the surroundings of plantations and their ability to spread into these areas (Hewitt and Kellman, 2002). On the other hand, many broadleaved species seem to regenerate better under coniferous than broadleaved canopy (Götmark et al., 2005). The coniferous canopy suppresses the growth of competitive herb vegetation, resulting in favorable conditions for shade-tolerant tree species.

Beech (*Fagus sylvatica*) and oaks (*Quercus robur*, *Q. petraea*), originally the dominant tree species in temperate Europe, are probably the most common target species. They are able to spread over long distances (Mosandl and Kleinert, 1998) and establish under coniferous canopy (Götmark et al., 2005). Short-lived pioneer

woody species, such as rowan (*Sorbus aucuparia*), birches (*Betula pendula* et *pubescens*) and Glossy buckthorn (*Frangula alnus*), can be of special importance, because of their ability to actively influence their environment by improving soil conditions in coniferous plantations (Emmer et al., 1998). Kreyer and Zerbe (2006) found a positive effect of these species on plant species diversity in pine plantations and concluded that these species can be indicators for plant diversity assessment within forest restoration processes.

Aims and contents of the thesis

The main aims of the thesis were: (1) to describe natural regeneration and vegetation changes in mountain spruce forests affected by bark beetle outbreak in comparison with stands where interventions against bark beetle were applied, and (2) to evaluate the possibilities of natural regeneration of indigenous species in coniferous plantations, which should be transformed to mixed stands.

Mountain spruce forests affected by a large-scale bark beetle outbreak were studied in the Šumava National Park (Czech Republic). These forests are one of the most extensive spruce forests in Central Europe, partly unmanaged and partly with interventions against bark beetle. The research was conducted in mountain spruce forests with completely dead canopy, waterlogged spruce forests with partly dead canopy, and clearcut stands with interventions against bark beetle. The particular aim was to compare the effect of non-interventional and interventional strategies from the ecological viewpoint.

Coniferous plantations, composed mostly of spruce, were studied in the province of Drenthe in the Netherlands. These stands represent a typical example of plantations outside the natural range of spruce, in an area where spruce was introduced as an exotic species. Nowadays, the plantations are being transformed, while natural regeneration of indigenous species tried as one of the transformation methods.

Chapter II presents the results of a five-year monitoring of natural regeneration in 18 permanent research plots in mountain spruce forests in the Šumava Mts. Mountain spruce forests with dead canopy, clearcut areas, and waterlogged spruce forests with partly dead canopy were compared. Detailed data about tree seedling numbers, their height and age structure, and microhabitat preferences are presented. Conclusions are made regarding the future development of the forests.

Chapter III presents the results from a one-year monitoring of natural regeneration of mountain waterlogged spruce forests in the Šumava Mts. The

study was conducted along 107 transects, comparing among (i) undisturbed stands, (ii) stands partly dead due to natural disturbances, (iii) clearcuts created by salvage logging, and (iv) sanitation stands, where trees attacked by bark beetle were cut down, debarked and left at the site.

Chapter IV presents the results about ground layer changes in the 18 permanent research plots described in Chapter II. The expansion and decline of particular herb and moss species are evaluated and discussed.

Chapter V presents the results of natural regeneration of indigenous species in spruce plantations in the Netherlands. Seedling numbers were recorded in 91 plots and are presented in relation to forestry management measures (gaps of various size, thinning) and the distance to seed sources.

Chapter VI contains a summary of the results presented in the previous chapters, and conclusions and generalizations based on them.

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Chapter II

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

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

Abstract

In the 1990's, 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 were 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.

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

Introduction

The bark beetle *Ips typographus* (L.) and some other bark beetle species are integral parts of any natural Norway 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 more easily (e.g. Berryman, 1986; Barbosa and Wagner, 1989; Tunset et al., 1993; Byers, 1996; Jakus, 1998). By creating space for a new generation 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 occurred 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 (Kiener, 1990; Bibelriether, 1991; Bibelriether et al., 1995; Strunz, 1994). Results from research on the development of such affected forest were presented by Fischer et al. (1990), Fischer (1992), Nüßlein and Faißt (1998), Mosandl and Fischer (1999), Huber (2000), Heurich (2001), and Jehl (2001). 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; Hullen et al., 1994; Bücking, 1997; 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 1990's, 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.

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 sea 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).

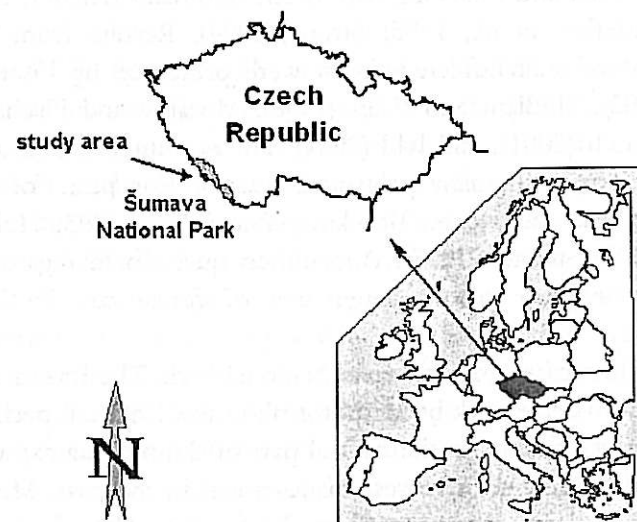


Fig. 1. The location of the study area within the Czech Republic and within Europe.

The forests in the studied area can be included into the alliance *Piceion excelsae* Pawlowski in Pawlowski, Sokolowski et 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* sp. 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.

Methods

Research plots

Eighteen 400 m² 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),
2. 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).

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. ≤ 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.

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.

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: $\ln(1 + \text{seedling number})$. 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).

Results*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 – 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.

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.

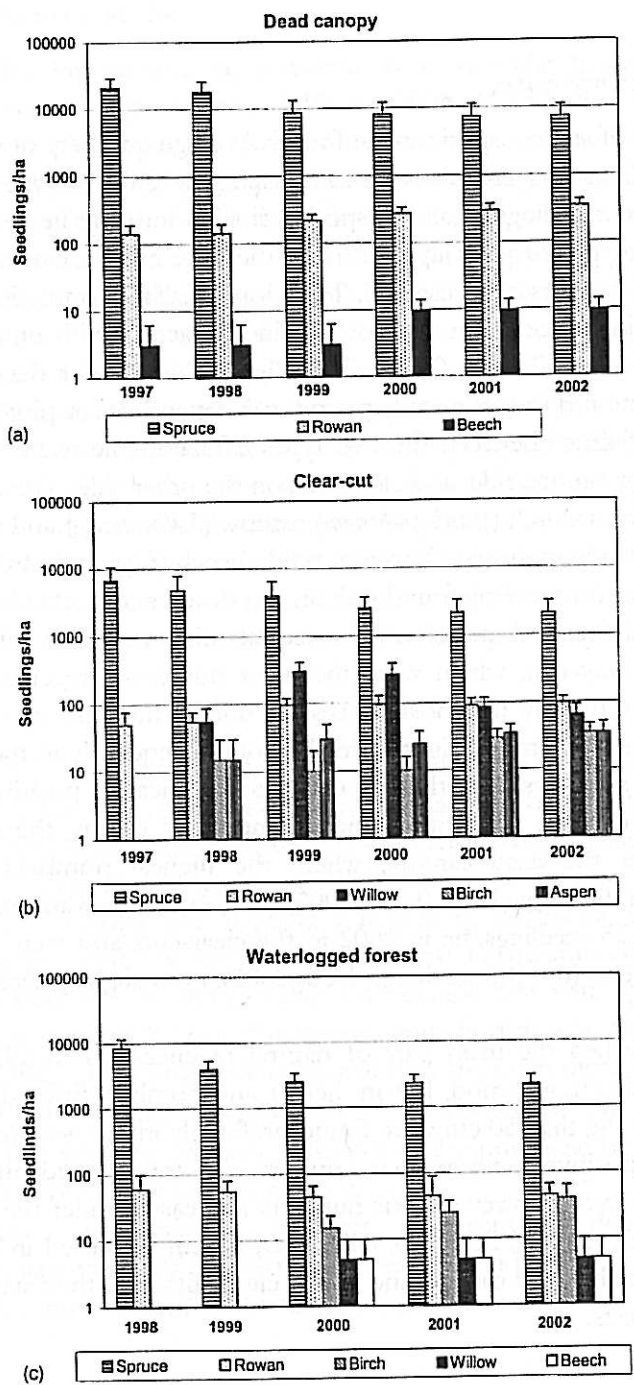


Fig. 2. (a-c) Average numbers of seedlings of the particular species per hectare in each year of observation in three types of plots.

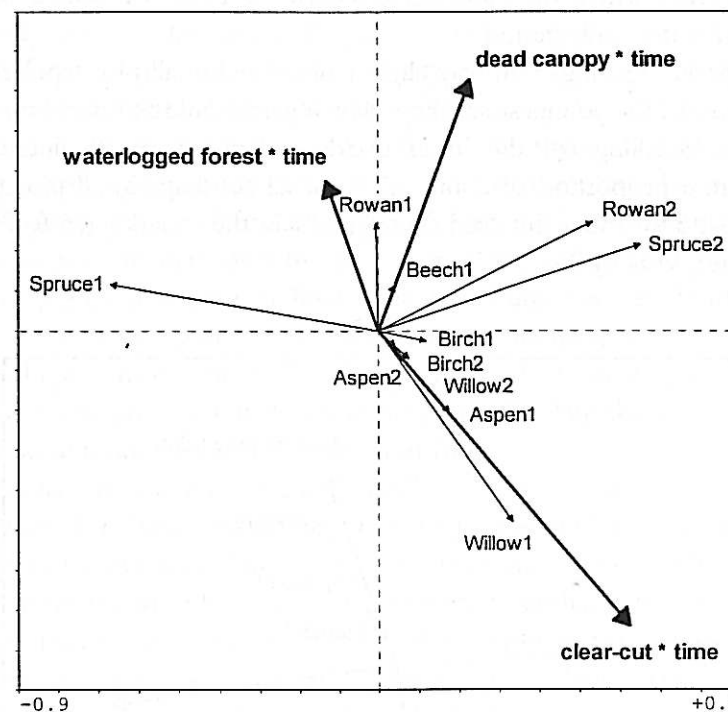


Fig. 3. Relationship between numbers of seedlings and type of plot in interaction with time (RDA analysis, $F = 11.43$, $p = 0.001$). Seedlings were classified into height categories: Spruce1, Rowan1, Beech1, Aspen1, Birch1, Willow1 - seedlings ≤ 50 cm; Spruce2, Rowan2, Aspen2, Birch2, Willow2 - seedlings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

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 clear-cuts, 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 1990's. 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.

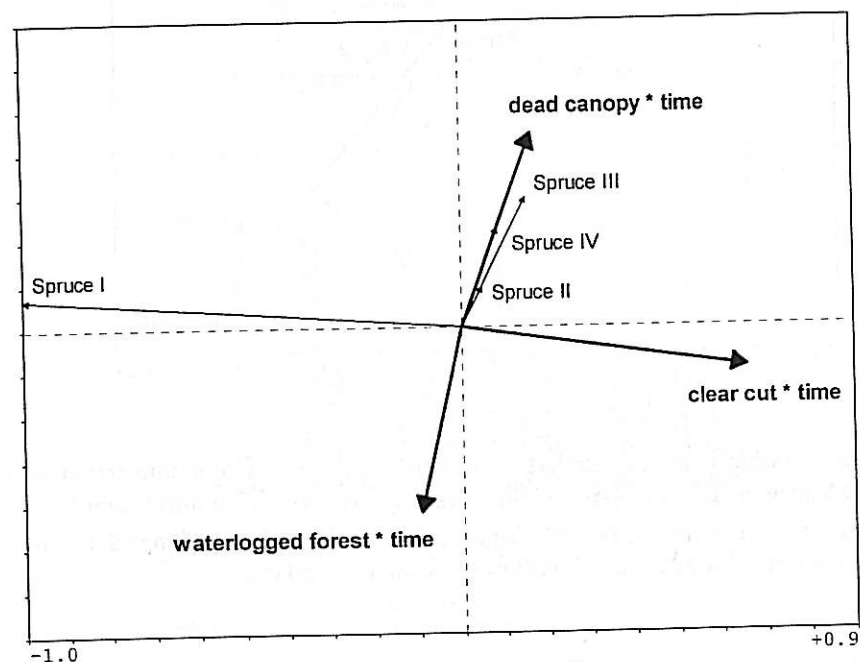


Fig. 4. Relationship between numbers of spruce seedlings and plot type in interaction with time (RDA analysis, $F = 22.62$, $p = 0.001$). The seedlings were classified into age-categories. Spruce I = < 5, Spruce II = 6 – 10, Spruce III = 11 – 20, Spruce IV = >20 years old seedlings.

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 m²) 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 *Calamagrostis villosa* and *Deschampsia flexuosa*) was least favourable microhabitat, especially for the youngest seedlings. Seedling densities were 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.

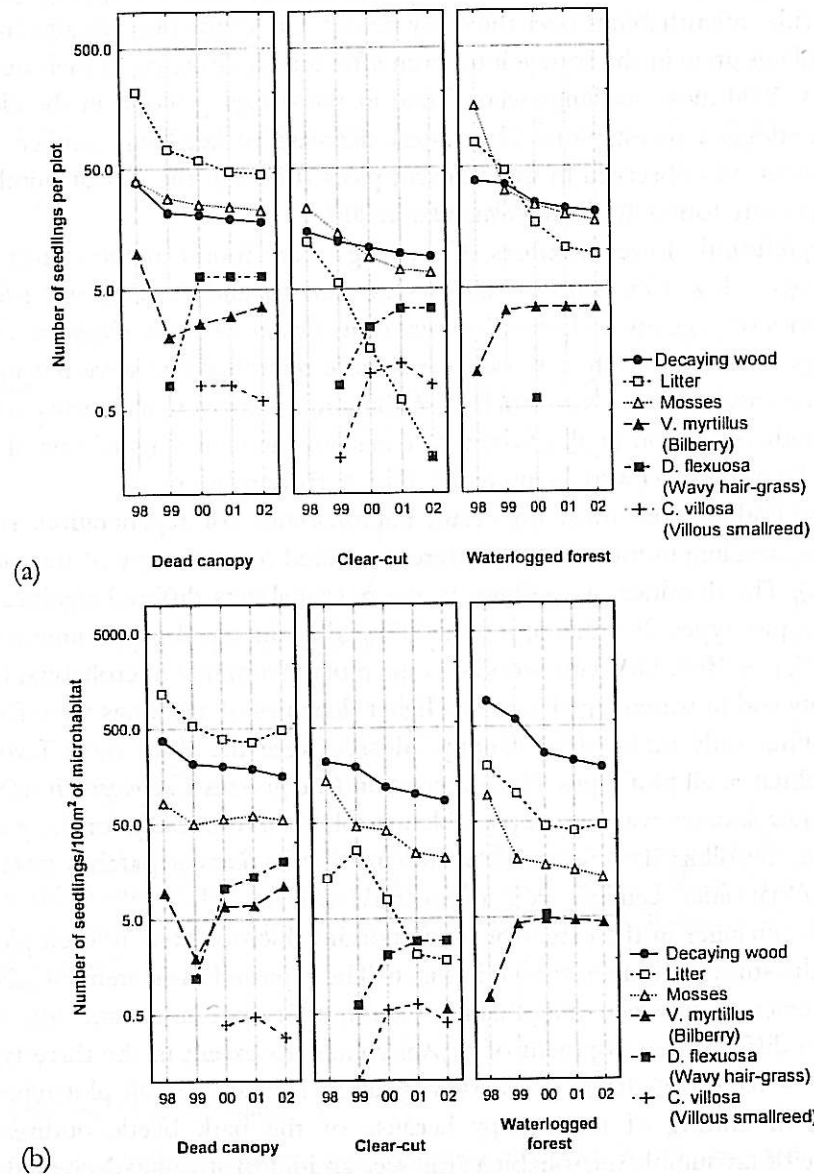


Fig. 5. (a and b) Total numbers of spruce seedlings in the experimental plots of 400 m² (a) and in 100 m² of the respective microhabitats (b).

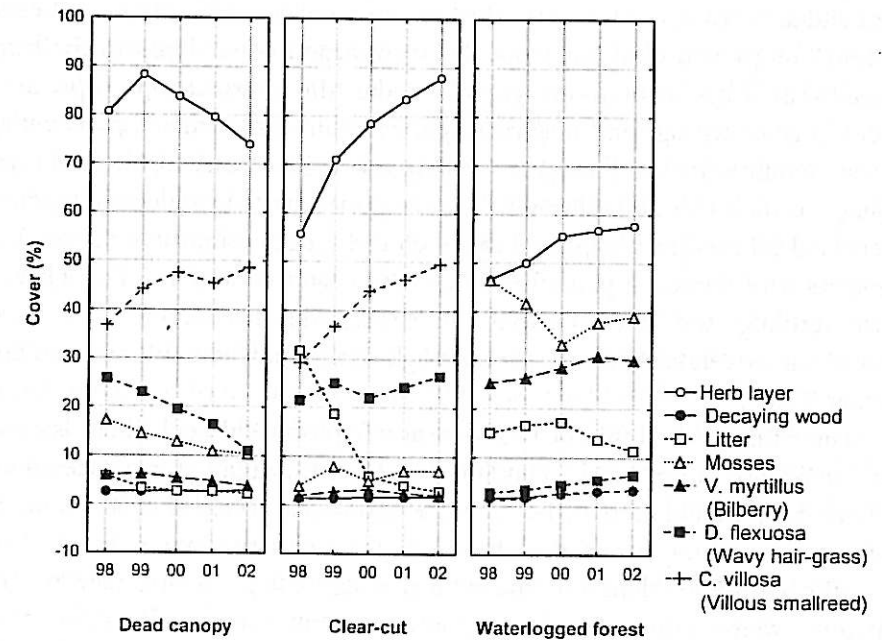


Fig. 6. Changes in covers of the particular microhabitats during the period of observation.

Discussion

Amount of natural regeneration

The results showed that in comparison with clear-cuts 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 ha 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 clear-cuts 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 Szwaagrzyk, 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; Kaňák, 1999).

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 (Sofron, 1981; Neuhäuslová, 2001). 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 (Ohlson and Zackrisson, 1992; Hornberg et al., 1997).

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; Szewczyk and Szwagrzyk, 1996; Hornberg et al., 1997) 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.

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.

Acknowledgements

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Chapter III

Natural regeneration and vegetation changes of waterlogged spruce forests after natural and artificial disturbances

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[manuscript]

Natural regeneration and vegetation changes of waterlogged spruce forests after natural and artificial disturbances

Abstract

An extensive area of mountain spruce (*Picea abies* (L.) Karst.) forests, including waterlogged forests, in the Šumava Mts., Central Europe, has been affected by a massive bark beetle (*Ips typographus* (L.)) outbreak since the middle of the 1990s. A part of the area was left without interventions and two types of interventions have been applied in other parts: (1) the classical forest approach based on the logging of attacked trees and (2) a "sanitation", in which attacked trees were cut down, debarked and left lying in the stand. The main goal of our research was to test the impact of non-intervention and both types of intervention on the further development and regeneration of waterlogged spruce forests. Detailed data about tree seedling abundance, percent cover of microhabitats and vegetation were collected in undisturbed stands (tree canopy > 25%), stands substantially influenced by natural disturbances (tree canopy < 25%, reduced by bark beetle outbreaks, partly windfalls), and stands influenced by artificial disturbances represented by clear-cut areas and sanitation stands. The spruce forests influenced by natural disturbances regenerated very well if left without interventions. The bark beetle and windfalls do not represent a threat to the long-term persistence of the forests. Clearcuts resulted in formation of pioneer stages with a postponed spruce regeneration. In sanitation stands, the reduction of both previous vegetation and tree regeneration was obvious. Generally, both interventions against bark beetle delayed restoration of waterlogged spruce forests.

Key words: mountain forest, bark beetle outbreak, natural regeneration, seedling recruitment, disturbances

Introduction

Tree species recruitment after disturbances is a key phenomenon for forest ecosystem development, because disturbances are essential for the regeneration of many tree species (Pontailler et al., 1997; Ulanova, 2000). Extensive bark beetle outbreaks are one of the most noticeable disturbances in Central European spruce forests, being similar to large-scale insect outbreaks frequently occurring in boreal forests (Larsen, 1980; Bonan and Shugart, 1989). In Central Europe, there is still a lack of knowledge about the development of natural spruce forests. One of the main reasons for this is that there are almost no strictly natural spruce forests preserved. Most of them were affected by anthropogenic factors such as air pollution and classical forest management leading to their unification and ecological destabilization. Moreover, bark beetle was commonly suppressed by tree cutting and windfalls were cleared even in protected areas. An extensive forest area affected by large-scale windfalls with subsequent bark beetle outbreaks was left without interventions for the first time in the Bayerischer Wald National Park, Germany (Bibelriether, 1989). Another similar situation, when the possibility of leaving a forest area without interventions, occurred in the Swiss Alps in the 1990's. Here a large bark-beetle outbreak, which was triggered by a windstorm event, caused the death of almost all spruce trees in an approximately 100 ha area (Lässig, 1995).

Waterlogged spruce forests in the Šumava Mts. are some of the best preserved and least influenced spruce forests in this geographical region. They also serve as refugia for several rare and endangered plant and animal species. Observation of their natural succession after a massive bark beetle attack can be a unique chance to understand natural processes in the Central European mountain spruce forests in general. Unfortunately, large interventions against bark beetle were made in the core zone of the Šumava National Park. Besides classical clearcutting, also a "sanitation" was used, in which attacked trees were cut down, debarked and left lying in the stand. As lying dead wood is an important part of natural forests (Kuuluvainen et al., 1998), it was supposed that natural biodiversity could be maintained if the silvicultural treatment simulated natural processes. However, the effects of interventions on forest ecosystem have seldom been particularly studied. Foster and Orwig (2006) found a great negative impact of salvage logging on forest ecosystem in New England compared to the impact of natural disturbances. Similar impact should be considered also in the case of Central-European forests.

In both cases of natural and artificial disturbances, it is likely that there were changes in natural regeneration structure due to changed canopy cover and, consequently, light conditions. Light conditions represent one of the most important factors determining the success of natural regeneration (e.g. Dai, 1996; Coates, 2002). Disturbances can create favorable microhabitats for establishment and growth of tree seedlings (e.g. Hofgaard, 1993a; Szewczyk and Szwagrzyk, 1996; Kuuluvainen and Kalmari, 2003). Nevertheless, artificial disturbances, such as clearcutting, differ in many aspects from natural ones. For example, there is almost no dead wood left compared to natural disturbances. Dead wood represents a very important microhabitat for spruce regeneration (Kupferschmid and Bugmann, 2005). Moreover, Fischer and Jehl (1999) found lying stems as obstacles for ungulates, and accessibility of the stand was found to be an even more important factor for browsing intensity than game numbers (Reimoser and Gossow, 1996). Consequently, clearcuts usually need to be re-planted with the planted trees suffering from browsing more than saplings originating from natural regeneration (Reimoser and Gossow, 1996; Bergström and Bergqvist, 1997). Every possible impact on natural regeneration can be substantial because natural regeneration is considered to be more vigorous and important for the maintenance of high genetic diversity compare to plantings (Lefèvre, 2004).

Changes in tree canopy are usually accompanied by changes in the forest understory (Vacek et al., 1999). Immediate changes in herb and moss layer composition can be expected after cutting operations (Jalonen and Vanha-Majamaa, 2001; Økland et al., 2003).

Our study compared changes in forest dynamics and development after both natural and artificial disturbances, i.e. dying trees after bark beetle outbreaks and windstorms versus interventions against bark beetle. The aim was to evaluate regeneration possibilities based on tree seedling establishment related to (1) the type of management and (2) the extent of microhabitat types. Relationship between management type and vegetation composition was also evaluated.

Study area

The research was carried out in the central part of the Šumava Mountains (Fig.1), in sites of natural and semi-natural waterlogged spruce forests. The altitude ranged between 1000 and 1275 m a. s. l. The area belongs to the cold climatic region with mean annual precipitation about 1500 mm and mean annual temperature about 4°C (Quitt, 1971). The bedrock is predominantly created by

gneiss, partly combined with granodiorites. Histosols and gleysols are the prevailing soil type under waterlogged spruce forests (Novák, 1989-1993).

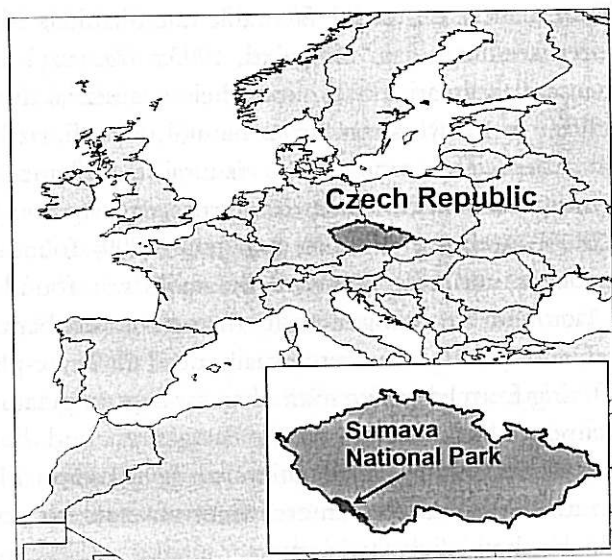


Fig. 1. The location of the study area within the Czech Republic and Europe.

The studied forests represent waterlogged spruce forests edaphically conditioned to cold and wet depressions and loose spruce forests occupying the margins of peat bogs characterized by the co-existence of species of the bog communities with species typical of the spruce forests. The tree layer consists practically only of spruce (*Picea abies*) owing to the permanently waterlogged soil. Birch (*Betula carpatica*) only rarely occurs as an admixture and rowan (*Sorbus aucuparia*) is found sporadically at stand edges. Herb layer cover is usually below 50%. *Vaccinium myrtillus* is dominant in the herb layer, while *Avenella flexuosa*, *Vaccinium vitis-idaea* and *Calamagrostis villosa* can be found as accompanying species with high constancy. *Triantalis europea*, *Homogyne alpina*, *Lycopodium annotinum*, *Soldanella montana*, *Eriophorum vaginatum*, *Carex nigra*, *Listera cordata* are also often found. The moss layer is well developed, typically with *Bazzania trilobata*, *Sphagnum* sp. div. and *Polytrichum commune* (Moravec et al., 2002).

The first logging interventions in the area, without a serious influence on the forests, are reported from the 17th century. The first important interventions, which significantly influenced and changed the forest structure, started at the

beginning of the 19th century (Pišta, 1972). These activities influenced especially the climax spruce forests, which occur here in a mosaic with waterlogged spruce forests. Spruce monocultures, planted after cutting, wind throws and bark beetle outbreaks, are predominant now on sites of the former climax spruce forests. The localities of waterlogged spruce forests were influenced rather little owing to their limited access on wet soils and now they represent the most valuable and preserved spruce stands in the mountains.

Methods

Research plots

A total of 107 transects (10 x 100 m) were established upright to a level line in selected stands and five 100 m² sample plots were regularly placed in each transect. The transects were selected to represent stands with different shares of dead canopy as a result of natural disturbances, especially bark beetle, and with or without interventions against bark beetle. According to these criteria, plots were divided into four groups.

Plots without interventions:

- (1) Green canopy, i.e. unmanaged stands composed namely of live trees, tree canopy cover > 25% (115 plots).
- (2) Dead canopy, i.e. dead and partly dead stands with tree canopy reduced by natural disturbances: bark beetle attack and partly uncleared wind throws, tree canopy cover < 25% (155 plots). Trees died gradually, mostly from 1994 to 2002.

Plots with interventions against bark beetle:

- (3) Clearcuts, i.e. plots without canopy (attacked by bark beetle, completely cut down), 0 – 25% of cut debarked trees left lying on the site (174 plots). Cutting in 1995 – 2001.
- (4) "Sanitation" stands without canopy, i.e. trees attacked by bark beetle were cut down, debarked, and left on the site (91 plots). Sanitation was performed in 1997 – 2001.

Data collecting

Tree canopy cover was evaluated in the 100 m² plots. Natural regeneration was measured by recording the numbers of seedlings of all tree species in inner plots of 3 x 3 m. Seedlings were divided into the following height categories: (a)

Spruce – 1. < 10 cm, 2. 10-20 cm, 3. 20-100 cm, 4. 100-300 cm. (b) Seedlings of broadleaves – 1. < 20 cm, 2. 20-50 cm, 3. 50-100 cm, 4. 100-300 cm.

Microhabitat types covering the forest floor were defined and their extent recorded in each 3 x 3 m plot. The analyzed microhabitats included laying debarked logs, laying non-debarked logs, patches of herb species, *Sphagnum* sp. patches, patches of other mosses in total, root plates, brushwood and litter. The extent of each microhabitat was determined by visually estimating their percent cover in each plot.

Vegetation was evaluated by visually estimating percent covers of particular herb species and the moss layer (divided into *Sphagnum* sp. and other mosses) in the inner plots.

Statistics

Seedling recruitment, for the tree species split into height categories, was analyzed by multivariate analysis using Canoco (Ter Braak and Šmilauer, 1998). Constrained ordination (Redundancy analysis, RDA) was used to identify the variability in species data that can be explained by explanatory variables. Management (includes the four plot types and crown canopy cover) and microhabitats (extents of particular microhabitats) were used as explanatory variables. The influence of altitude was eliminated by using it as a covariable. The influence of time elapsed from intervention was evaluated in separate analyses for data from clearcuts and sanitation plots. The total effect of time and the possible different effect of the two types of intervention on seedling numbers were tested. Square-root transformed seedling numbers of particular tree species were used as response (species) data. The linear model of species response was selected (RDA) based on the length of the gradient that measures the beta diversity in species composition along the ordination axes. This gradient was determined from the results of a preliminary weighted-averaging method with detrending as described by Lepš and Šmilauer (2003). The value of the gradient was shorter than 1, so the linear method was selected. The statistical significance of the relation with explanatory variables was tested by Monte Carlo permutation test. The resulting ordination diagrams were produced using CanoDraw (Ter Braak and Šmilauer, 1998).

Vegetation pattern in relation to the management regimes was also evaluated by Redundancy Analysis (RDA). Covers of herb layer species were used as response (species) data, and management regime types were used as explanatory variables. The influence of time from intervention was evaluated only

for data from intervention plots in the same way as in the case of natural regeneration.

Differences in seedling numbers of spruce and rowan, extent of microhabitat types, average number of species per plot, and average number of forest species per plot among plot types were tested by one-way ANOVA (Statistica 6.0 program). In case of significant effects ($p < 0.05$), post-hoc comparisons were made using the Tukey HSD test.

Results

Multivariate analysis of natural regeneration of tree species

Seedlings of five tree species were found. RDA analysis showed the significant influence of management (type of plot, canopy cover), microhabitats, and time elapsed from human intervention (Table 1). The effect of time did not differ between clearcuts and sanitation plots (non-significant interaction between time and type of plot). The number of seedlings of all species related to the compared types of stands and canopy cover are shown in Figure 2. The greatest difference appeared between the plots without intervention under both types of canopy (dead and green) on one side and plots with management against bark beetle on the other. All height categories of wind-dispersed pioneer species (*Salix* sp. div., *Betula* sp. div. and *Populus tremula*) were strictly correlated with plots managed against bark beetle. Spruce (*Picea abies*) and rowan (*Sorbus aucuparia*) seedlings were prevalent under the canopy. Rowan and taller spruce seedlings preferred canopy < 25% (dead stands), while spruce seedlings of lower height-categories were prevalent under canopy > 25% (green stands).

The relationship between various microhabitat types and tree species seedlings are shown by the RDA analysis results in Figure 3. The first ordination axis separated all broadleaved species, except for rowan of the lowest height-category, from spruce seedlings of all height-categories. Spruce seedlings were correlated with non-debarked logs, root plates, mosses including *Sphagnum* species and a lower herb layer cover. Broadleaved species dominated in plots with brushwood, debarked logs and a higher herb layer cover. Microhabitats explained the greatest part of the variability in the species data (28.1%).

Time elapsed from intervention seemed to be the less important factor, explaining only 1.1% of variability in the data from the intervention plots. The effect of time did not differ between clearcuts and sanitation plots (not significant

interaction). Time had a slight positive influence on the number of seedlings of higher height categories, especially rowan, willow, and birch.

Table 1. Summary of RDA analyses. Expl. variability = percentage of the total variability in species data that can be explained by each group of environmental variables. Correl. 1st axis = species-environment correlations for the first RDA axis.

Analysis	Used data	Tested variables	Expl. variability	Correl. 1st axis	p-value
<i>Natural regeneration:</i>					
I.	all plots	Management (plot type, canopy cover)	13.2	0.457	0.001
II.	all plots	Microhabitats	28.1	0.633	0.001
III.	clearcuts and sanitized plots	Intervention time	1.1	0.164	0.014
IV.	clearcuts and sanitized plots	Intervention type x Intervention time			not significant
<i>Vegetation:</i>					
V.	all plots	Management (plot type, canopy cover)	8.1	0.444	0.001
VI.	clearcuts and sanitized plots	Intervention time	3.7	0.373	0.002
VII.	clearcuts and sanitized plots	Intervention type x Intervention time			not significant

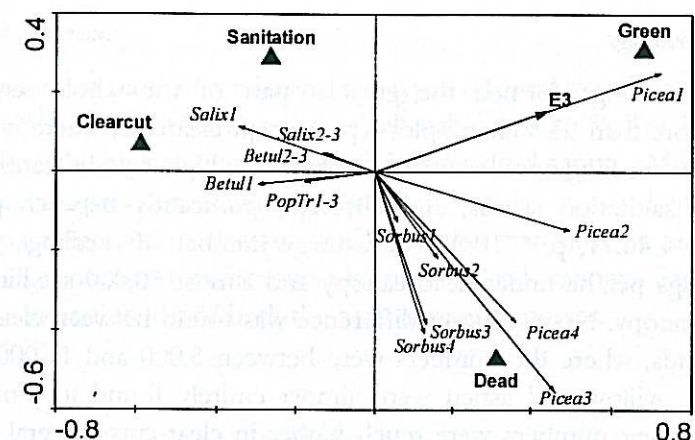


Fig. 2. RDA analysis: numbers of seedlings divided into height categories (in italics) in relation to the type of plot (green canopy, dead canopy, clearcut, sanitation) and canopy cover (E3). Abbreviations of species names: *Picea* – *Picea abies*, *Sorbus* – *Sorbus aucuparia*, *Salix* – *Salix* sp., *Betul* – *Betula* sp., *PopTr* – *Populus tremula*. Indication of height categories: *Picea abies*: 1 = < 10 cm, 2 = 10 - 20 cm, 3 = 20 - 100 cm, 4 = 100 - 300 cm. Other species: 1 = < 20 cm, 2 = 20 - 50 cm, 3 = 50 - 100 cm, 4 = 100 - 300 cm.

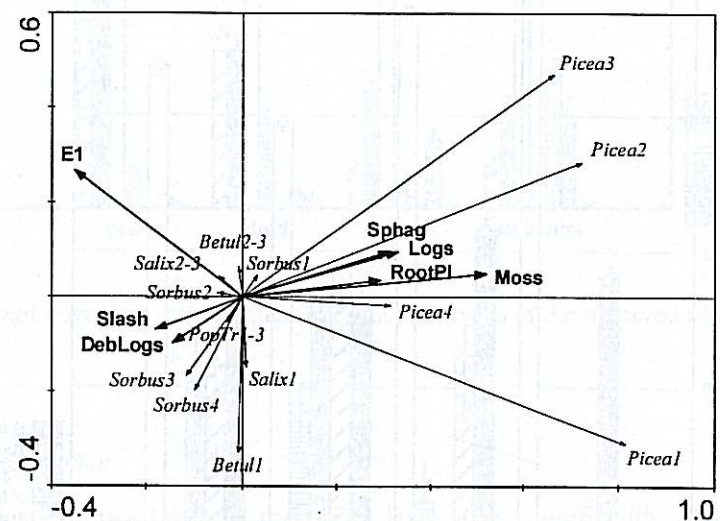


Fig. 3. RDA analysis: number of seedlings divided into height categories (in italics) in relation to covers of microhabitats. Abbreviations of microhabitat names: E1 – herb layer, Slash – slash wood, DebLogs – debarked logs, Logs – non-debarked logs, RootPl – root plates, Moss – mosses except *Sphagnum* species, Sphag – *Sphagnum* species. Abbreviations of species names – see Fig. 2.

Number of tree seedlings

Spruce seedlings formed the greatest part of the whole regeneration, comprising more than 97 % in all plot types except clearcuts, where it was 83 % (Fig. 4). Spruce seedling numbers were several times higher under canopy than in clearcuts and sanitation stands, and differed significantly between plot types (ANOVA, $F = 46.71$, $p < 10^{-6}$). The average number of seedlings was about 30,000 seedlings per ha under dead canopy and almost 50,000 seedlings per ha under green canopy. No significant difference was found between clear-cuts and sanitation stands, where the numbers were between 5,000 and 11,000 seedlings per ha. Birch, willow and aspen were almost entirely found in plots without canopy. Also, their numbers were much higher in clear-cuts (several hundreds) than in sanitation plots (about 70 seedlings per ha). Rowan had a different occurrence from other broadleaves. Significantly highest numbers were found under dead canopy (more than 700 seedlings per ha, ANOVA, $F = 6.28$, $p = 0.0003$), while similar numbers were found in all other types of plots: about 200 in plots without canopy and 300 seedlings per ha under green canopy. Some beech seedlings (*Fagus sylvatica*) were found in some stands with dead canopy, but outside of our plots.

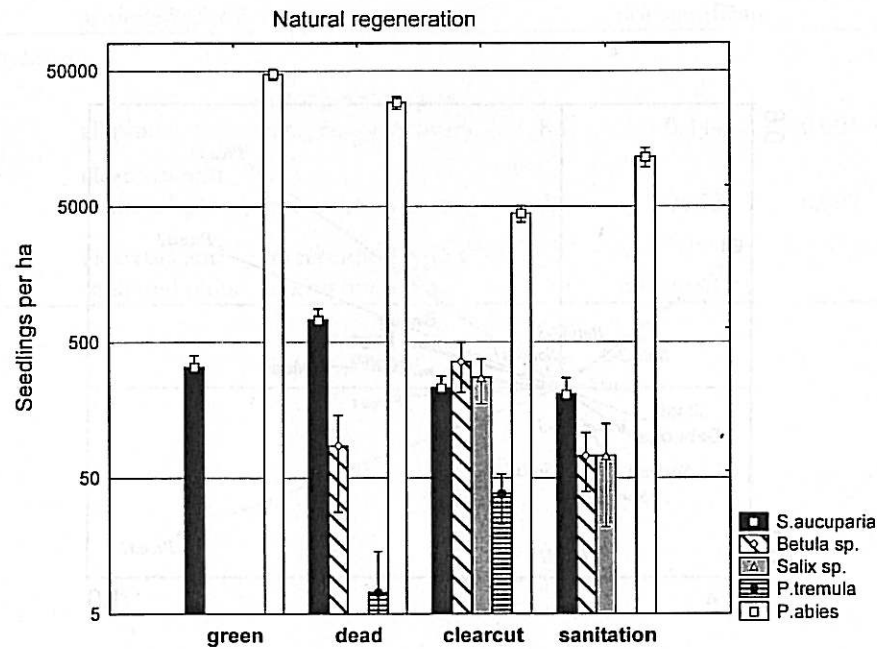


Fig. 4. Average number of seedlings of particular species per ha in the observed plot types.

Microhabitat occurrence

The cover of particular microhabitat types differed significantly among plot types (ANOVA, $p < 10^{-6}$ in the case of all habitats, Fig. 5). Total cover of the herb layer was the highest in clear-cuts and under dead canopy. Mosses including *Sphagnum* sp. were prevalent under green canopy, but also survived quite well under dead canopy compared to clearcuts and sanitation stands. Root plates and non-debarked logs occurred predominantly under dead canopy. Sanitation plots featured the lowest covers of both the herb layer and mosses.

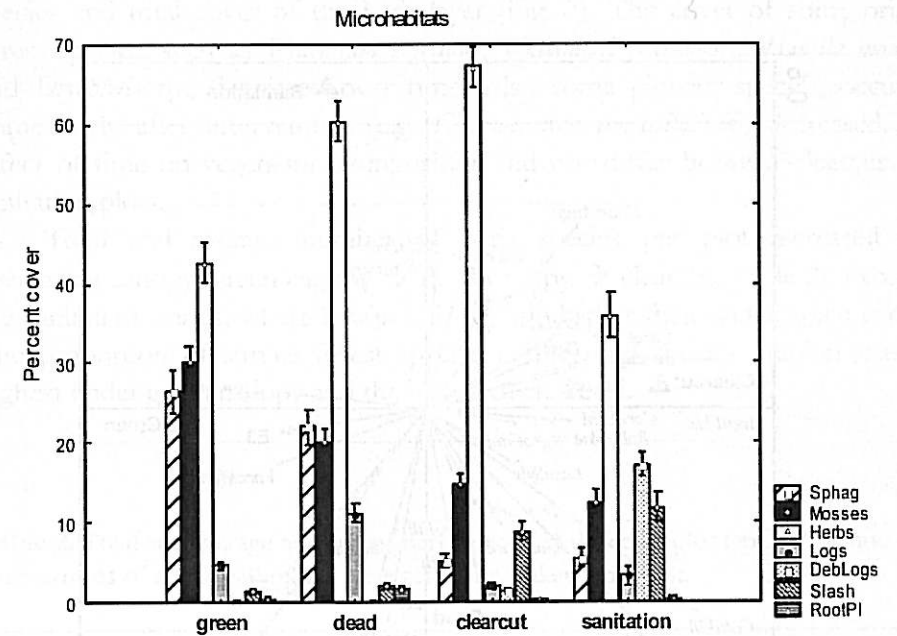


Fig. 5. Percent covers of the particular microhabitat types in the observed plot types.

Vegetation composition

Species composition of the herb layer was significantly influenced by management and, in the intervention plots, by the time elapsed from the intervention (Table 1). Vegetation composition seems to be less influenced by environmental factors than natural regeneration of tree species (a lower part of

the explained variability in the vegetation data than in the natural regeneration data). Species typical of spruce forests were found in plots under both green and dead canopy (Fig. 6). *Lycopodium annotinum* and *Vaccinium myrtillus* occurred in high covers under green canopy. *Oxalis acetosella*, *Calamagrostis villosa*, *Trientalis europea*, *Galium harynicum*, and the ferns *Dryopteris dilata* and *Athyrium filix-femina* dominated in less closed dead stands. Species typically found in clearcuts were *Rubus idaeus*, graminoids such as *Calamagrostis villosa*, *Avenella flexuosa* and *Luzula sylvatica*, and also *Carex canescens* and *C. echinata* in strongly waterlogged sites. Species of spruce forests were almost absent in sanitation stands; the species found were typical also of clearcuts (*Chamaenerion angustifolium*, *Rubus* sp.).

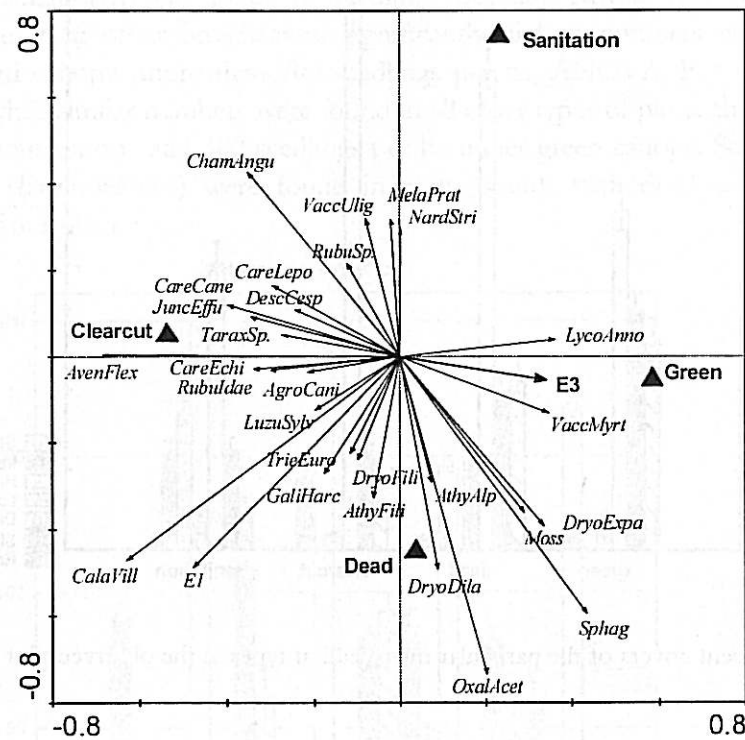


Fig. 6. RDA analysis: cover of herb layer species and mosses in total in relation to the type of plot (green, dead, clearcut, sanitated) and canopy cover (E3). Species names abbreviations: AgroCani – *Agrostis canina*, AthyAlp – *Athyrium alpestris*, AvenFlex – *Avenella flexuosa*, CallaVill – *Calamagrostis villosa*, CareCane – *Carex canescens*, CareEchi – *Carex echinata*, CareLepo – *Carex Leporina*, ChamAngu – *Chamaenerion angustifolium*, DescCesp – *Deschampsia cespitosa*, DryoDila – *Dryopteris dilatata*, DryoExpa –

Dryopteris expansa, DryoFili – *Dryopteris filix-mas*, AthyFili – *Athyrium filix-femina*, Galiharc – *Galium harynicum*, JuncEffu – *Juncus effusus*, LuzuSylv – *Luzula sylvatica*, LycoAnno – *Lycopodium annotinum*, MelaPrat – *Melampyrum pratense*, Moss – mosses, NardStri – *Nardus stricta*, OxalAcet – *Oxalis acetosella*, RubuIdae – *Rubus idaeus*, RubuSp. – *Rubus* sp., Sphag – *Sphagnum* sp., TaraxSp. – *Taraxacum* sp., TrieEuro – *Trientalis europea*, VaccMyrt – *Vaccinium myrtillus*, VaccUlig – *Vaccinium uliginosum*, E1 – total herb layer cover.

The time elapsed from intervention influenced positively the increase of *Galium harynicum*, *Avenella flexuosa*, *Calamagrostis villosa*, *Luzula sylvatica*, *Rubus* species and total cover of the herb layer (Fig. 7). The cover of some original forest species, such as *Vaccinium myrtillus*, *Vaccinium vitis-idea*, *Soldanella montana*, and *Dryopteris* sp., decreased over time. Also some pioneer species, occurring immediately after intervention (e.g. *Chamaenerion angustifolium*), decreased. The effect of time on vegetation composition did not differ between clearcuts and sanitation plots.

Total and average number of herb species per plot increased with decreasing canopy (green canopy → dead canopy → clearcut, Table 2), except in the sanitation stands, where it was only slightly higher than under green canopy. The proportion of spruce forest species in the total species number was the highest under green canopy and the lowest in clearcuts.

Table 2. Total and average number of herb species in different plot types. Post-hoc comparisons of average numbers were tested by Tukey HSD test.

	green	dead	clearcut	sanitation
Total number of species found in particular type of plot	30	44	69	36
Percentage of forest species in total number of species	46.7	34.1	23.2	38.9
Average number of species found in a plot (3 x 3 m)	4.1 ^a	5.6 ^b	6.5 ^c	4.6 ^a

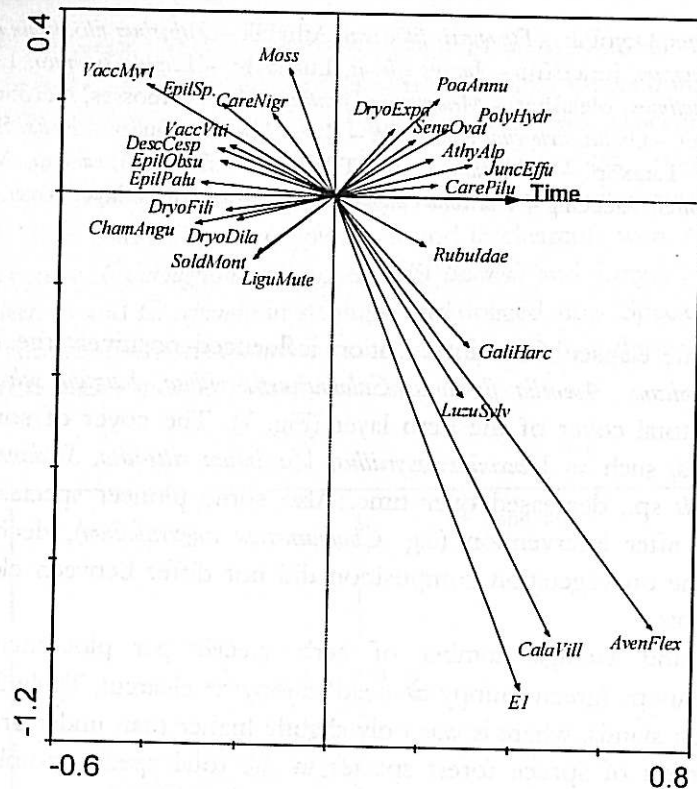


Fig. 7. RDA analysis: covers of herb layer species in clearcuts and sanitation plots in relation to the time elapsed from intervention against bark beetle. Species names abbreviations same as in Fig. 6.

Discussion

The influence of plot type on natural regeneration

The type of disturbance significantly influenced the natural regeneration structure in the studied waterlogged spruce forests. Spruce formed the greatest part of regeneration in all types of plots, but preferred plots with green canopy. This result is different from those obtained in previously managed mountain spruce forests, where more spruce seedlings were found under dead than green

canopy (Nüßlein and Faißt, 1998; Reif and Przybilla, 1998). The same applies for natural boreal spruce forests, where canopy gaps are crucial for the successful establishment of spruce (Leemans, 1991; Drobyshev, 1999). Nevertheless, the studied waterlogged spruce forests had a relatively open canopy, which may be the reason why canopy reduction after bark beetle attack did not have the same positive effect on spruce regeneration as in previously managed mountain spruce forests with a relatively closed canopy. Moreover, there are more suitable microhabitats in waterlogged spruce forests, so the numbers of seedlings, especially in low age categories, are often higher than in mountain spruce forests. In disturbed plots, the highest number of spruce were found under dead canopy, the second highest in sanitation plots and the lowest numbers were in clearcuts. It is probable that the spruce seedling numbers decrease with increasing disturbance of the soil surface: bark beetle attacks resulted in more open canopy and, in comparison with artificial disturbances, almost did not influence the soil surface. The low numbers in clearcuts were probably caused by spruce sensitivity to removal cutting, which usually results in a high mortality in spruce seedlings (Nilsson et al., 2002). Leaving debarked logs in plots seems to be a better option than clearcuts for spruce regeneration. Nevertheless, both types of intervention against bark beetle caused a great reduction of spruce regeneration compared to dead stands, and consequently a limitation of natural selection can be expected. Natural selection is the key factor for the establishment of new spatially structured stands resistant to disturbances, because seedling development, especially in the mountains, depends on the synergistic influence of multiple stresses, which leads to survival of the most adapted seedlings (Modrzyński, 1995; Sera et al., 2000). Moreover, spruce produces seeds only periodically in extreme mountain conditions and, although periodic regeneration is sufficient for maintenance of the forest (Hofgaard, 1993b), we found that interventions against bark beetle largely reduced the youngest generations of seedlings in mountain spruce forests (Jonášová and Prach, 2004).

Rowan was the most numerous broadleaved species and, as the only species, had its highest numbers under dead canopy. In contrast to the other observed species, it has a great ability to be spread by birds over large distances (Leder, 1997). Clearcuts and sanitation stands are not so attractive for birds, which limited the spread of rowan in the study site. Vanha-Majamaa et al. (1996) also recorded the highest regeneration of rowan in forest areas, particularly in the shade of dead trees. Open canopy is necessary for its growth and flowering, although seedlings and saplings are tolerant of shade (Grime et al., 1988). Increasing rowan numbers seems to be a typical phenomenon in stands after bark

beetle attack. Its importance for natural regeneration in damaged spruce stands was reported by Weihs (1995) and Leder (1996)).

Other broadleaved species (birch, willow, aspen) clearly prevailed in clearcuts, with only a minor number of seedlings being found under dead canopy and in sanitation stands. These species are very light demanding and are considered as pioneers in succession (Grime et al., 1988). Lässig (1995) found an increasing number of pioneer broadleaved species with increasing size of clearings. In our case, light conditions in the clearcuts and sanitation stands were the same, because their area was similar and the tree layer was completely removed in both of them. The lower number of pioneer broadleaved species in sanitation stands can probably be attributed to a lack of favorable microhabitats.

The influence of microhabitat structure on natural regeneration

Favorable microhabitat structure appeared to be a key factor for successful regeneration of waterlogged spruce forests. This is supported by the results of the RDA analysis, where microhabitats explained more of the variability in the species data than plot type. Consequently, it is likely that the structure of regeneration was influenced more by a suitable structure of microhabitats than canopy closure. The occurrence of spruce seedlings was correlated with non-debarked logs, mosses and root plates. These microhabitats seem to be the same as are found in natural spruce forests: rotten wood is most often reported as a favorable habitat (Szewczyk and Szwagrzyk, 1996; Hornberg et al., 1997; Kupferschmid and Bugmann, 2005; Valkonen and Maguire, 2005). Further favorable microhabitats are mosses (Parker et al., 1997; Hanssen, 2003; Hunziker and Brang, 2005) and disturbed surfaces such as mounds and uprooted trees (Ulanova, 2000).

The results for broadleaved species were not so clear, although they were found mostly in plots with brushwood, debarked logs and herbs. These conditions are typically found in plots with interventions against bark beetle, where also soil disturbance is assumed to occur. The establishment of wind-dispersed broadleaved species with light seeds, such as birch (contrary to spruce or rowan), is partly dependent on bare soil (Perala and Alm, 1990; Nillson et al., 2002). This microhabitat was not recorded, because it is usually overgrown by herb vegetation very soon after cutting. However, tree species probably had a chance to establish before closing by the herb layer. Rowan is not known to prefer some special microhabitat, nevertheless, brushwood and parts of dead trees are important for all broadleaved species as protection against browsing, which is a common problem in this region (Matějková and Jonášová, 2002).

The extent of microhabitat types was influenced by interventions against bark beetle. Sites after the natural disturbance (bark beetle) are more similar to undisturbed stands in this respect than to sites after the artificial disturbance (intervention against bark beetle). Favorable microhabitats for spruce, such as mosses, non-debarked logs and root plates, were predominant under both green and dead canopy. The change in microhabitat structure under dead canopy appears to be very slow compared to change caused by artificial disturbances. Shading by snags seems to be an important factor under dead canopy, moderating the changes caused by canopy reduction.

The extent of favorable microhabitats for spruce decreased in clearcuts while the extent of unfavorable ones, i.e. especially herb layer, increased. The most severe change occurred with wood removal, resulting in the loss of potential microhabitats for spruce seedling establishment. Dead wood, besides large living trees and snags, is one of the most important components of natural spruce forests and, at the same time, the slowest component of the natural forest structure to recover (Siitonen et al., 2000). Its importance is now acknowledged even in production forests (Meyer, 1999). Kuuluvainen et al. (1998) reported the mean volume of decaying logs on the forest floor as between 35 – 113 % of the living tree volume. This can be achieved in the future after decay of dead wood formed from a bark beetle attack. In this respect, bark beetles act as positive factors in the development of a more natural forest structure.

Unfavorable microhabitats, such as debarked logs and brushwood, abounded in sanitation plots. Contrary to non-debarked logs, where seedlings can establish in the bark, debarked logs can act as suitable microhabitats only after they are decayed. It takes decades for logs to decay (Zielonka and Piątek, 2004) and even longer time can be expected in the case of debarked logs, which tend to dry up.

Vegetation composition

Relative light level, controlled by the tree canopy dynamics, is a key factor determining the dynamics of the herb layer (Nabuurs, 1996). In our plots, the number of light demanding species increased with decreasing tree canopy, except in sanitation stands, where the number was similar as under green canopy. These species had probably better conditions to establish in clearcuts, where soil disturbance occurred after logging operations. The total number of species and the number of species per plot were also highest in clearcuts, which corresponds to other results (e.g. Pykälä, 2004). Fischer et al. (1990) found twice as many species in cleared and uncleared windthrow, and under dead canopy, than under

adjacent green canopy. These results indicate that total species number cannot be used as an indicator of the condition of a community, because human disturbance led to increased number of weedy species at the expense of late successional species. We found that also forest species cover increased slightly under dead canopy and in clearcuts. Nevertheless, this increase was caused by only a few graminoid species, such as *Avenella flexuosa*, *Calamagrostis villosa* and *Luzula sylvatica*. The share of species typical of spruce forests in total species number was the lowest in clearcuts. Among other plants, mosses were the most sensitive to disturbance (Jalonen and Vanha-Majamaa, 2001). Their rapid decrease in clearcuts and sanitation stands compared to dead stands showed the relatively low influence of bark beetle on moss abundance compared to artificial disturbances.

Fischer et al. (1990, 2002) found that dead wood after a windfall is important for forest vegetation: ground vegetation of the uncleared windfall areas differed little from that of the previous undisturbed spruce forest. Herb vegetation in the cleared windfall areas, which had intensive soil-surface disturbance, due to the removal of the damaged wood, resembled the vegetation that develops after logging; species composition changed towards pioneer herb and tree species (birch). There was some resemblance between uncleared windfalls and sanitation stands in this study, but sanitation seems to have more destructive effects on vegetation. The covers of mosses and herbs largely decreased, but pioneer species did not strongly establish. Other observations of sanitation stand dynamics are needed.

Conclusions

Based on this study, it seems that man is not capable of simulating natural processes in mountain forests. The results of artificial disturbances differed distinctly from natural disturbances. Natural disturbance encouraged natural regeneration of the original species of spruce forests without leading to extensive changes in vegetation structure. On the contrary, both observed types of interventions against bark beetle substantially damaged the forest ecosystem. Although sanitation was supported by forest management as being close to nature, its results are largely different compared to natural disturbance. The conditions in sanitation stands are not favorable either for regeneration of the original species, such as dead canopy, or for wind-dispersed pioneer species, like in clearcuts. Nevertheless, sanitation still appears as a better choice than clearcutting in maintaining the forest community: spruce seedlings survived here

more successfully than in clearcuts and pioneer vegetation did not expand. Thus, sanitation should be carried out only in border zones of the Šumava National Park instead of classical clearcutting to prevent bark beetle spreading to adjacent commercial spruce stands.

Generally, both types of interventions can be thought of as counterproductive. Disturbance caused by bark beetle attack had a positive effect on original species regeneration and helps to recover the natural forest structure. The non-intervention strategy should be preferred in protected areas as much as possible over technical forestry interventions.

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View of a part of the study area in the bark beetle attacked mountain spruce forests with intervention areas (Šumava Mts.) (A), interior of dead stands with amounts of dead wood (B), surviving endangered species *Streptopus amplexifolius* (C), and abundant regeneration of spruce and rowan (D).



A clearcut area shortly after intervention against bark beetle (A), and after expansion of *Calamagrostis villosa* (B). Rowan (*Sorbus aucuparia*) suffering from browsing in clearcut (C).

Chapter IV

Central-European mountain spruce forests: the influence of bark beetle outbreak on the ground layer vegetation

Jonášová, M. and Prach, K.
[manuscript]

Central European mountain spruce forests: the influence of bark-beetle outbreak on the ground layer vegetation

Abstract

Changes in the herb and moss layers of mountain spruce (*Picea abies* (L.) Karst.) forests after bark beetle (*Ips typographus* (L.)) outbreak were compared with and without forestry intervention. The study area is situated in the Šumava National Park (Czech Republic), where an extensive bark beetle outbreak occurred in the 1990's. Parts of forests were left without interventions, while salvage logging was applied in other areas. Altogether, 18 permanent research plots were established in: (1) climax stands with completely dead canopy, (2) climax stands where salvage logging was applied (clearcuts), and (3) in more resistant waterlogged stands with only partly dead canopy. Vegetation composition, species numbers, and representation of life forms of species were evaluated between 1997 and 2002. Ellenberg indicator values were used as indirect estimators of environmental variability.

There was a severe effect of salvage logging on vegetation compared to the bark beetle outbreak itself. Forest herb species and partly also mosses survived relatively well under completely dead canopy. The least changes occurred under the partly dead canopy in waterlogged forests. The herb layer expanded in clearcuts originated due to salvage logging, being dominated by grasses. Mosses were more susceptible to disturbance than herbs; their cover in clearcuts was markedly lower and composition changed towards pioneer species. Direct disturbance of vegetation and soil surface due to logging operations seems to be an important factor enabling grass expansion and pioneer species establishment in clearcuts. The results show that a natural succession of mountain spruce forests after a bark beetle outbreak, if left without interventions, will probably avoid a pioneer stage and direct recovery of the forests will be possible. Salvage logging had negative effects on species composition, decreased forest recovery, and should not be permitted in the national park.

Keywords: bark beetle outbreak, understory vegetation, mountain spruce forests, salvage logging, forest succession, disturbance

Nomenclature: Vascular plants according to Kubát et al. (2002), mosses according to Kučera and Váňa (2003).

Introduction

Vegetation composition and species diversity of the herb layer closely interact with tree layer composition and structure (Schuck et al., 1994; Nabuurs, 1996; Holeksa, 2003). For this reason, the extensive mortality of mountain spruce forests by bark beetle (*Ips typographus* (L.)), which occurred in some Central-European mountains in the 1990's, could potentially lead to large-scale vegetation changes. Although bark beetle, together with storm events, is the most important natural factor determining the dynamics of mountain spruce forests (Schelhaas et al., 2003), long-term observations of natural succession of mountain spruce forests after bark beetle outbreak are rare. Most mountain spruce forests have not been preserved in a natural form. In addition, salvage logging has been the main management technique in Central Europe to deal with natural disturbances like wind and bark beetle. Salvage logging consists of felling infested trees, which often results in complete clearcutting. Extensive, near-natural spruce forests were left to develop naturally without any interventions for the first time in the Bayerischer Wald National Park in Germany after a windfall in 1980's destroyed the tree layer (Bibelriether et al., 1995). It was the first possibility in Europe to compare the natural succession of a forest ecosystem after windfall with a cleared area (Fischer and Jehl, 1999; Jehl, 2001). The development of vegetation and natural regeneration in large forest areas affected by windstorm were also studied in the Swiss Alps (Rammig et al., 2006). The first studies observing the natural development of European mountain spruce forests after bark beetle outbreak also occurred in the Bayerischer Wald (Heurich, 2001; Bauer, 2002).

Changes in forest understory vegetation can be expected due to anthropogenic disturbance in the form of salvage logging, which is still the most common approach to forests attacked by bark beetle. There is not enough information about this influence in comparison with a non-interventional approach, because the impact of salvage logging was frequently overlooked as an indirect impact of the outbreak (Foster and Orwig, 2006; Lindenmayer and Noss, 2006). Most studies investigated the influence of regular forest management, such as different types of cutting (e.g. Hannerz and Hånell, 1997; Pykälä, 2004; Kern et al., 2006). Clearcutting, which is the most common form of salvage logging, was generally found to have the strongest influence on vegetation (e.g. Roberts and Zhu, 2002). After clearcutting, the flora is usually dominated by early successional species with especially some late successional plant species becoming locally extinct (Hannerz and Hånell, 1997; Godefroid et al., 2005). Significant vegetation changes occurred even with partial cutting (Deal, 2001) and thinning (Brunet et

al., 1996). The influence of forest management on ground layer species composition can be stronger than the influence of soil and microclimate (Aude and Lawesson, 1998).

The effect of salvage logging can be considerably different from the effect of natural disturbance. The most common form of salvage logging is felling and removing all trees in infested stand (Wermelinger, 2004), which results in extreme changes in light conditions. Changes in infested stands left without interventions are much slower, because attacked trees remain standing for a few years and the canopy is reduced gradually. The importance of even a reduced canopy for maintaining favorable microclimatic conditions (Heithecker and Halpern, 2006) and survival of forest species and tree regeneration is known (Hannerz and Hånell, 1997). Salvage logging can be expected to result in direct mechanical disturbance of vegetation, tree regeneration and soil surface by logging operations. The lack of dead wood after salvage logging is a basic difference compared to natural disturbance. This can greatly affect the future natural dynamics of spruce forests. Dead wood is an essential part of the dynamics of mountain spruce forests and represents the most important microsite for spruce seedlings (Jonášová and Prach, 2004; Svoboda, 2005). Salvage logging can have more severe effects on forests than logging within regular management, where the importance of dead wood has already been recognized and other forms than clearcutting have been recently applied (Koch and Skovsgaard, 1999).

Forests of the Šumava Mountains (Bohemian Forest, Czech Republic) and Bayerischer Wald (Bavarian Forest, German side of the border) form the most extensive forest complex in Central Europe. The area is protected by two national parks: the Šumava National Park in the Czech part and the Bayerischer Wald National Park in the German part of the mountains. A large complex of mountain spruce forests situated in the central part of the mountains was affected by a bark beetle outbreak in the 1990's. A non-intervention approach was used in Bayerischer Wald and some small adjacent parts of the Šumava Mts. Interventions against the bark beetle in the form of salvage logging were applied in other parts of the Šumava Mts. This study was performed as part of a long-term observation of permanent research plots located in spruce forests affected by bark beetle with and without interventions. The first results about natural regeneration of tree species have already been published (Jonášová and Prach, 2004). This study aims to answer the following questions: What are the differences and changes over time in (1) the ground layer, (2) plant species diversity, and (3) environmental conditions in spruce forests affected by bark beetle outbreak left without interventions compared to stands where salvage logging was applied? Some

implications of the results are outlined in regards to restoration of mountain spruce forests.

Methods

Study area

The study area was in the central part of the Šumava Mts. in the Modrava region, approximately between the Lusen and Rachel peaks (48° 56' – 48° 59' N, 13°25' – 13° 29' E). The altitude of the research plots ranged from 1175 to 1280 m a. s. l. The area is a cold climatic region (Quitt, 1971), with a very short, cold and humid summer and a very long, cold and humid winter with abundant and long-lasting snow cover. Mean annual precipitation is about 1500 mm and mean annual temperature about 4°C. The bedrock is predominantly gneiss, partly combined with granodiorites. Podzols are the prevailing soil type under climax mountain spruce forests; histosols and gleysols occur under waterlogged spruce forests (Novák, 1989-1993).

The area is covered by extensive complexes of both natural and management influenced spruce forests. Climax mountain spruce forests occur in a mosaic with edaphically conditioned waterlogged and peaty spruce forests and treeless peat bogs. In the past, some beech (*Fagus sylvatica*) was probably admixed at lower altitudes (Neuhäuslová, 2001), but spruce has always been dominant because of the inclement climatic conditions. The current spruce forests originated partly from planting and sowing in clearcuts after windstorm and bark beetle calamities in the 19th century (Jelínek, 1988). Waterlogged and peaty spruce forests have remained the least influenced by management.

The studied forests belong to the alliance *Piceion excelsae*. The unit includes acidophilous climax mountain spruce forests and edaphically conditioned waterlogged spruce forests (Neuhäuslová, 2001). Climax mountain spruce forests are represented by the association *Calamagrostio villosae-Piceetum* with the tree layer dominated almost exclusively by spruce (*Picea abies*). Rowan (*Sorbus aucuparia*) grows often on edges and in open sites. Acidophilous herbs, such as *Callamagrostis villosa*, *Avenella flexuosa*, and *Vaccinium myrtillus*, dominate in the herb layer. *Homogyne alpina*, *Trientalis europea*, *Luzula sylvatica*, and *Dryopteris dilatata* are also frequently present. The dominant moss species are *Polytrichastrum formosum*, *Dicranum scoparium*, and *Sphagnum girgensohnii*.

The waterlogged spruce forests are represented by the associations *Bazzanio-Piceetum* and *Sphagno-Piceetum*. The tree layer consists only of spruce owing to the

permanently waterlogged soil. Herb layer cover is usually below 50%. *Vaccinium myrtillus* is dominant in the herb layer, while *Avenella flexuosa*, *Vaccinium vitis-idaea* and *Calamagrostis villosa* can also be found with higher constancy. *Trientalis europea*, *Homogyne alpina*, *Lycopodium annotinum*, *Soldanella montana*, and *Listera cordata* are present with low constancy and dominance. The moss layer is well developed typically with *Bazzania trilobata* and *Sphagnum* sp. div. Additional species of bog communities (*Eriophorum vaginatum*, *Carex nigra*) and *Polytrichum commune* in the moss layer are present in the *Sphagno-Piceetum* (Moravec et al., 2002).

Research plots

Altogether, 18 permanent research plots, 400 m² each, were selected in representative parts of available stands of spruce forests both with and without interventions. The plots were established in three types of stands:

1. Dead canopy, i.e. climax mountain spruce forest, which was attacked by bark beetle in 1997 resulting in spruce mortality, left without interventions. The canopy cover was reduced from 41% on average in 1997, i.e. shortly after the bark beetle attack, to 11.5% in 2002 (visually estimated) due to the natural falling of parts of dead trees. Eight plots were established.
2. Clear-cut climax mountain spruce forest, which was attacked by bark beetle and completely cut in 1997. Five plots were established.
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 were established.

Only mature, relatively homogenous stands of mountain and waterlogged spruce forests were selected for the study. The tree layer was formed only by spruce, with the initial crown canopy of about 50%. Herb and moss layers in the plots were formed by the typical plant and moss species of these forest communities (see above).

Data collecting

Percentage covers of particular herb and moss species and covers of tree, herb, and moss layers were visually estimated in each plot. For this purpose, each plot was divided into 4 subplots of 100 m² and the covers were evaluated in each subplot separately. This division was made in order to obtain a more precise estimation. For further processing, pooled data from the whole plot were used to

avoid pseudoreplications (Hurlbert 1984). Herb species and total cover of particular layers were evaluated annually from 1997 to 2002, while moss species were evaluated only in 1997, 1998 and 2002.

The first detailed evaluation was made in the climax spruce forests in 1997 immediately after tree death in dead plots or clearcuts. Preliminary vegetation evaluation was made before mortality or cutting, to select comparable plots. Plot evaluation in waterlogged spruce forests started in 1998. We assumed little change in the vegetation since 1997, because these plots were alive and were partly attacked by bark beetle only in 1998. The regeneration of tree species was evaluated in detail separately in the other part of the study, and the results were published elsewhere (Jonášová and Prach, 2004).

Statistics

Vegetation composition was evaluated by multivariate methods using Canoco for Windows (ter Braak and Šmilauer, 1998). Square-root transformed data were used, and data on herb and moss species covers were evaluated separately. Based on the gradient length from a preliminary Detrended Correspondence Analysis, the method based on a linear model was used. The data were first evaluated by Principal Component Analysis (PCA), which involved the whole variability of data on species covers. Environmental variables (plot type, crown cover, time) were displayed post-hoc in the ordination space. Redundancy Analysis (RDA) was then used. Plot type, crown cover, and time were used as environmental variables in the first RDA analysis (Analysis I). Altitude was used as a covariate. This was followed by several partial analyses, where the influence of particular environmental variables was eliminated by using them as covariates, and the percent variability in the species data explained by particular environmental variables was identified (Analyses II – IV). Then the interaction of plot type with time was tested, which tests the null hypothesis that the temporal trend in the species composition is independent of plot type (Analysis V).

The changes in herb and moss layer covers and cover of typical species of mountain spruce forests among plot types during the observed time period were tested by repeated measure ANOVA. Typical species of spruce forests were reconsidered as diagnostic, constant, and dominant species, according to Chytrý and Tichý (2003).

Species diversity was expressed as the mean numbers of moss-, herb-, and typical species per plot. Their changes during the observed time period in plot types were tested by repeated measures ANOVA.

Life forms, after Raunkiaer, were used according to Ellenberg et al. (1991) as follows: C - herb chamaephyte, E - epiphyte, G - geophyte, H - hemicryptophyte, T - therophyte, Z - woody chamaephyte. Covers of particular life forms were counted for each plot, separately for herbs and mosses. Resultant covers were used as dependent variables in the RDA analysis and the differences among plot type over time were evaluated similarly as the previous RDA analyses on vegetation composition.

Environmental conditions were not directly measured. Instead, Ellenberg indicator values for light, temperature, soil moisture, pH, and nitrogen were used as indirect estimators of environmental variability (Ellenberg et al., 1991). All plots were characterized by the so-called Ellenberg indices, which were counted as weighted averages for all species in a plot, separately for herbs and mosses. Nitrogen was used only for herbs, because there are no Ellenberg values for mosses. The relationships between the Ellenberg indices and plot type and time were analyzed by several RDA analyses, where Ellenberg indices for particular plots were used as dependent variables.

Results

Vegetation composition:

PCA ordination separated the plots into distinct groups of samples by plot type (Figs. 1 and 2), with clearcuts and dead canopy in the left part of the diagram and waterlogged spruce forests in the right part. The results are somewhat different for herbs and mosses. The composition of the herb layer under dead canopy and in clearcuts did not differ very much at the beginning of the study. Nevertheless, further development of vegetation was rather different, as can be seen from the direction of the arrows in Figure 1a. The covers of the grasses *Calamagrostis villosa* and *Avenella flexuosa* increased and pioneer species (*Juncus effusus*, *Carex canescens*, *Rumex acetosella*, *Rubus idaeus*) appeared in clearcuts (Appendix I). Almost no pioneer species appeared under dead canopy and typical forest species, such as *Oxalis acetosella*, *Homogyne alpina*, and *Trientalis europaea*, even slightly increased. *Calamagrostis villosa* also increased under dead canopy, but *Avenella flexuosa* decreased, and the total cover of the herb layer did not change. The third most common typical species, *Vaccinium myrtillus*, only slightly decreased under the dead canopy. It had very low covers in clearcuts already in the first year of observation.

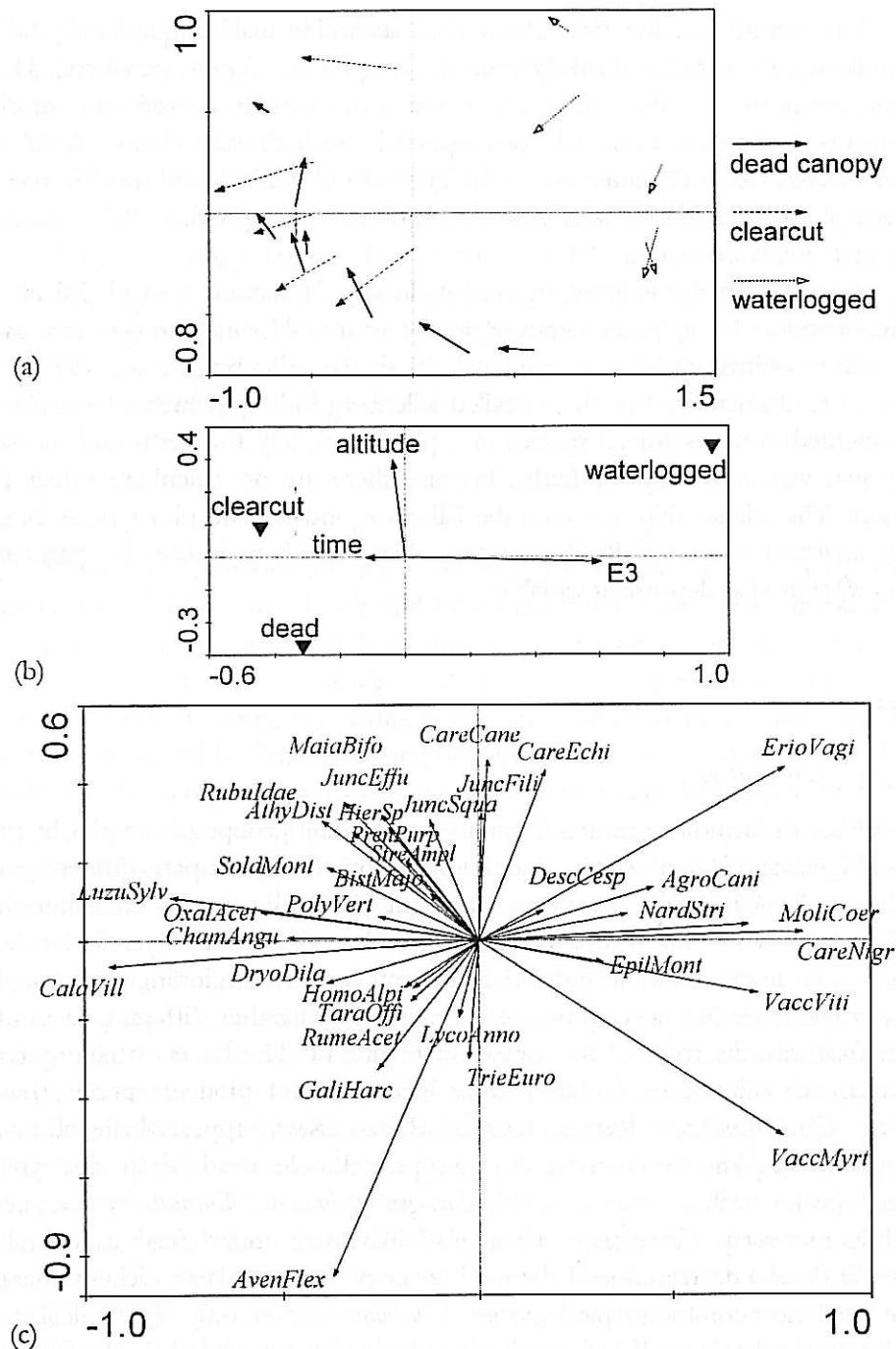


Fig. 1. (a-c) PCA ordination diagrams (herb layer) represent the projections of: (a) 18 research plots at the beginning and end of the observation period (shown as arrows indicating the direction of vegetation change between years for each plot), (b) species, and

(c) passively projected environmental variables. The species are labeled by the first four letters of the genus name and the first four letters of the species name (full species names are listed in Appendix I). The quantitative environmental variables are time, altitude, and tree canopy cover (E3). Type of plot is used as a categorical variable.

Waterlogged spruce forests exhibited somewhat different species composition of both herb and moss layers from the beginning. *Vaccinium myrtillus* dominated and even slightly increased in cover during the study. Partial dying of the tree layer resulted in only few changes in covers of other species. Species such as *Nardus stricta*, *Luzula sylvatica*, *Avenella flexuosa* and *Calamagrostis villosa* slightly increased their covers at the expense of moisture demanding *Carex* species. This partly increased the similarity of waterlogged plots with other plots (see the arrows in Fig. 1a).

Moss layer composition was rather different under dead canopy and in clearcuts from the beginning of the study (Fig. 2, Appendix II). This was obviously caused by a higher sensitivity of mosses to disturbance. Especially liverworts of the genera *Cahypogeia* and *Cephalozia* were missing in clearcuts. *Lophozia attenuata*, *L. floerkei*, and *L. longiflora* disappeared later. Pioneer species such as *Ceratodon purpureus*, *Funaria hygrometrica*, and *Polytrichum juniperinum* appeared instead. Most species survived under dead canopy, and no new pioneer species appeared. Waterlogged spruce forests were the most species-rich and all typical moss species of spruce forests were present in similar covers both at the beginning and end of the observation period. Only few changes were found in the case of other species.

The results of RDA analyses (Table 1) confirmed that the greatest amount of variability in species composition (both herbs and mosses) was explained by the type of plot (about 50%). Nevertheless, the effect of time and crown canopy was also significant. The significant effect of time indicates a similar temporal change in species composition in all plot types. This change is caused by a certain decrease of wet- and shade-demanding species and increase of light-demanding species in all the plots. The significant interaction between plot type and time implies also a temporal change in vegetation composition dependent on plot type.

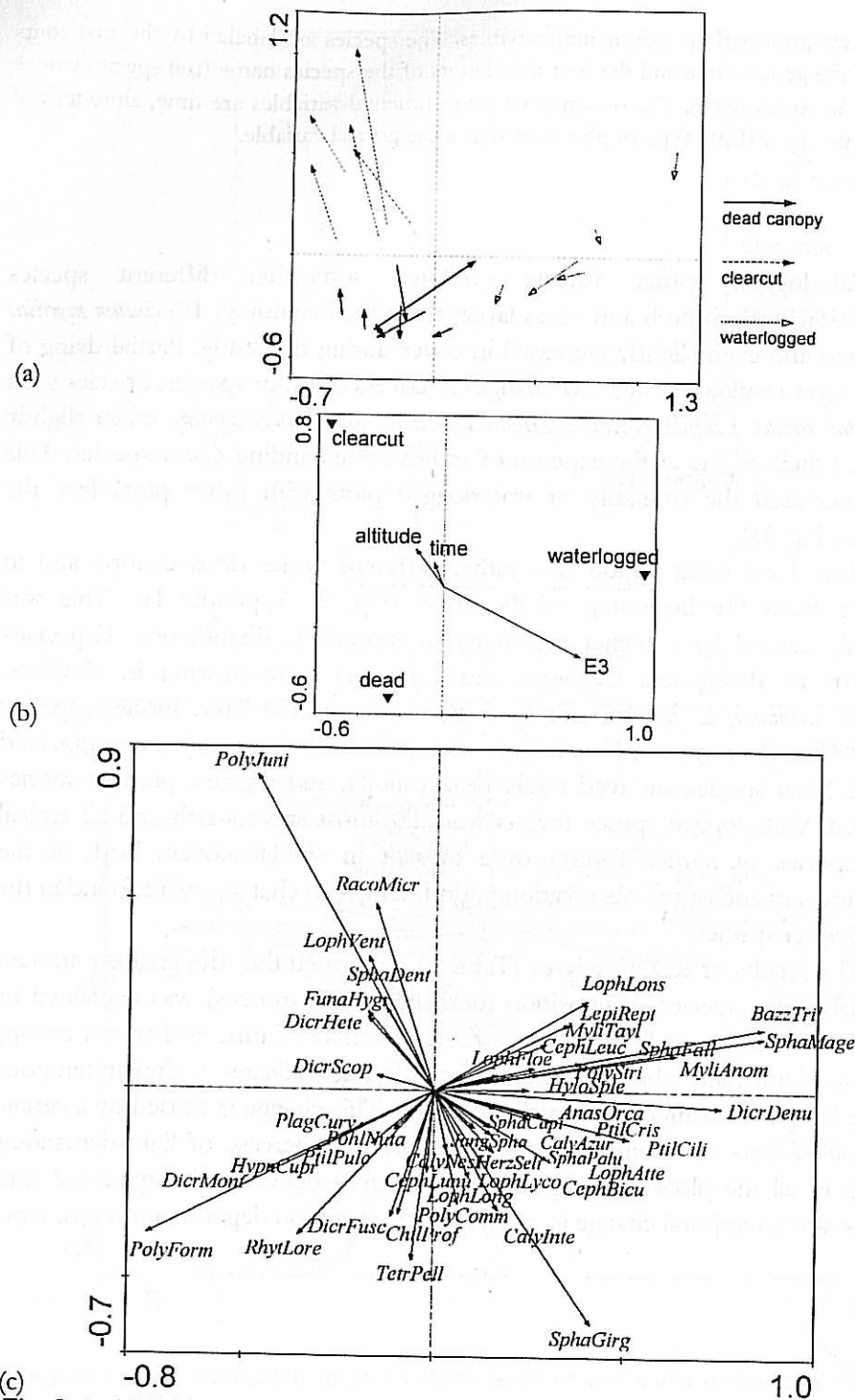


Fig. 2. (a-c) PCA ordination diagrams of moss layer composition. Full species names are listed in Appendix II. For other explanation see Fig. 1.

Table 1. Results of RDA analyses. Explained variability represents percentage of the total variation in the dependent data (herbs, mosses, Ellenberg indices, life forms) explained by particular explanatory variables.

Analysis	Explanatory variables	Covariables	Explained variability (%)			
			Herbs	Mosses	Ellenb	Life forms
I	plot type, time, E3	altitude	52.4	53.5	54.4	49.2
II	plot type	time, altitude	50.6	50.4	51.5	44.4
III	E3	plot	0.8	1.4	n.s.	1.8
IV	time	plot	1.1	1.5	1.4	3.9
V	dead*time, clear*time, water*time	plot, time	1.3	2.2	n.s.	4.4

Total covers of herb and moss layers and typical species

Total cover of the herb layer was the highest under dead canopy at the beginning of the study and it did not change during the observation period (Tables 2 and 3). It was lower in waterlogged forests and increased slightly during the observation period. The greatest change in herb layer cover occurred in clearcuts, where it doubled over the five years. Cover of the moss layer was the highest in waterlogged forests and the lowest in clearcuts. In waterlogged forests it decreased only slightly, while under dead canopy it decreased by less than half. It was very low in clearcuts at the beginning of the study and, although it slightly increased, it still remained about half as high as under dead canopy.

The cover of typical species differed significantly among plot types and also changed differently in plot types. At the beginning, it was the highest under dead canopy and the lowest in clearcuts. It decreased a bit under dead canopy and increased in waterlogged forests and especially in clearcuts so that it was rather similar at the end of the study. Nevertheless, the increase in clearcuts was almost exclusively caused by increased cover of the grasses *Calamagrostis villosa* and *Avenella flexuosa*.

Table 2. Mean (and standard deviation) cover of particular layers and number of species per 400 m² plot in the types of plots at the beginning and end of the observation period.

	Dead canopy		Clearcut		Waterlogged	
	1997	2002	1997	2002	1998	2002
Mean cover:						
Tree layer	40.9 ± 10.1	11.4 ± 3.5	0	0	50.0 ± 5.5	28.5 ± 5.3
Herb layer	75.2 ± 8.2	73.6 ± 7.7	43.8 ± 14.1	88.9 ± 2.7	46.6 ± 16.2	57.6 ± 21.3
Moss layer	19.5 ± 8.1	11.5 ± 3.9	6.5 ± 1.1	7.1 ± 1.9	46.5 ± 5.1	39.0 ± 5.6
Typical species	98.9 ± 5.8	87.7 ± 11.7	56.4 ± 18.8	85.8 ± 13.3	66.1 ± 16.6	76.7 ± 29.8
Mean numbers of species:						
Herbs	9.8 ± 1.4	12.0 ± 2.3	11.0 ± 2.1	12.4 ± 3.6	10.0 ± 2.9	12.2 ± 4.2
Mosses	15.6 ± 2.4	11.9 ± 2.8	13.6 ± 3.9	9.4 ± 2.4	18.8 ± 2.5	21.6 ± 3.9
Typical species	14.4 ± 1.1	13.5 ± 0.9	11.4 ± 1.7	9.8 ± 1.9	13.4 ± 2.7	14.0 ± 4.1

Number of species

A total of 36 herb and 57 moss species were found (Appendixes I and II). Among them were 3 endangered species of herbs (*Lycopodium annotinum*, *Soldanella montana*, *Streptopus amplexifolius*) (Procházka and Štech 2002) and 2 endangered species of mosses (*Bazzania tricrenata*, *Cephalozia leucantha*) (Kučera and Váňa 2003). Two species are indicated as rare and requiring more attention (*Athyrium distentifolium*, *Lophozia longidens*).

The total number of herb species did not differ significantly among plot types and increased slightly in all plot types over time (Tables 2 and 3). The number of mosses differed among plot types with changes over time also differing. The highest number was recorded in waterlogged plots and the lowest in clearcuts in all years. The number increased in waterlogged forest, but decreased in clearcuts and under dead canopy. The number of typical species of mountain spruce forests (herbs and mosses together) was significantly lower in clearcuts compared to dead canopy and waterlogged plots. Changes over time were not significant.

Table 3. The results of repeated measures ANOVA. Plot type, time and the interaction of plot type and time were tested as explanatory variables for particular dependent variables.

	Tested variables	F	p
Cover of herb species	Plot type	5.11	0.02
	Time	38.63	< 10 ⁻⁴
	Plot type x Time	23.48	< 10 ⁻⁴
Cover of moss species	Plot type	118.21	< 10 ⁻⁶
	Time	6.39	0.023
	Plot type x Time		n.s.
Cover of typical species	Plot type	3.61	0.05
	Time	13.27	0.002
	Plot type x Time	22.01	< 10 ⁻⁴
Number of herb species	Plot type		n.s.
	Time	12.95	0.003
	Plot type x Time		n.s.
Number of moss species	Plot type	16.26	0.0002
	Time		n.s.
	Plot type x Time	4.71	0.026
Number of typical species	Plot type	4.05	0.039
	Time		n.s.
	Plot type x Time		n.s.

Life forms

Herbs occurred as chamaephytes, geophytes, and hemicryptophytes, while mosses occurred as chamaephytes, hemicryptophytes, epiphytes, and therophytes. The covers of life forms were significantly influenced by all the tested variables, i.e. plot type, time, and crown cover. The interaction of plot type and time was also significant, which means that changes over time differed in plot types (Table 1). Type of plot accounted for the greatest part of the variability in the data. Herb geophytes, chamaephytes, and hemicryptophytes, and moss epiphytes dominated under dead canopy (Fig. 3a). High covers of herb hemicryptophytes and especially moss therophytes were dominant in clearcuts. The dominants in waterlogged

forests and under close canopy were represented by woody chamaephytes, and moss chamaephytes and hemicryptophytes. The covers of herb geophytes, chamaephytes, hemicryptophytes, and moss epiphytes generally increased over time. Temporal trends for particular plot types are displayed in Fig. 3b. Increase of cover of herb hemicryptophytes was typical for clearcuts. Herb geophytes and chamaephytes increased under dead canopy. The other life forms of mosses, i.e. chamaephytes, hemicryptophytes, and epiphytes, together with woody chamaephytes, increased in waterlogged forests.

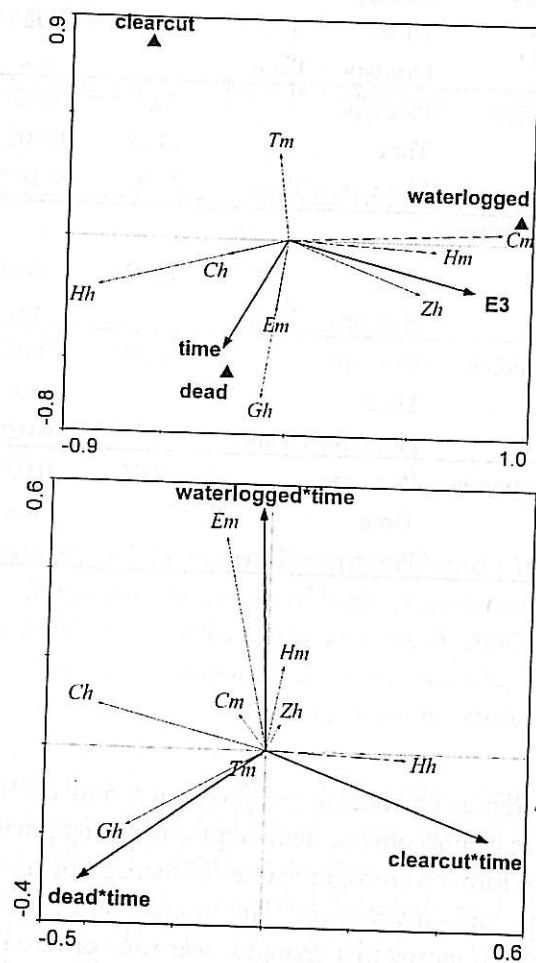


Fig. 3. (a and b) RDA species-environmental biplots with covers of life forms used as dependent variables (Analyses I and V, Table 1). Time, E3, and plot type (a) and the interaction of plot type with time (b) were used as environmental variables. Abbreviations of life forms: C - herb chamaephyte, E - epiphyte, G - geophyte, H - hemicryptophyte, T - therophyte, Z - woody chamaephyte. Herbs are indicated by *h*, mosses by *m*.

Ellenberg values

The values of Ellenberg indices can be best explained by plot type, which accounted for the greatest part of the variability (Table 1). There was also a significant temporal change in the same direction for all the plots. Temporal changes were not significantly different among plot types. The highest values for moisture and temperature indices (both herbs and mosses) were in waterlogged forests (Fig. 4). Indices for light were the lowest under dead canopy, but their values increased over time in all plot types. Herbs and mosses differed in pH indices. Herbs had the highest value under dead canopy, but mosses in clearcuts. Herbs also indicated the highest values of nitrogen under dead canopy. Slight temporal changes were found for nitrogen and pH indices, being different for herbs and mosses: values for nitrogen and pH decreased as indicated by herbs, while values for pH increased as indicated by mosses.

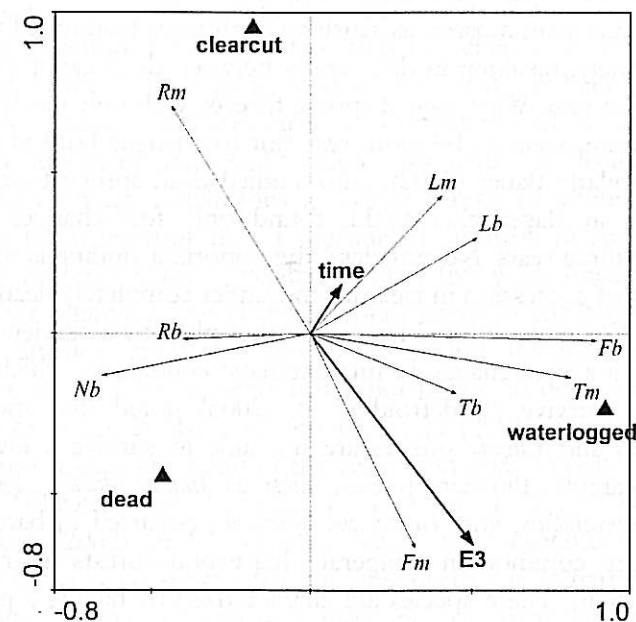


Fig. 4. RDA species-environmental biplot with Ellenberg indices used as dependent variables (Analysis I, Table 1). Time, E3, and plot type were used as environmental variables. Abbreviations of Ellenberg indices: L - light, F - moisture, T - temperature, R - pH, N - nitrogen. Indices for herbs are indicated by *h*, indices for mosses by *m*.

Discussion

Vegetation composition

Generally, a minor effect of time on vegetation composition was found in comparison with the effect of plot type. Also, particular plots within plot types differed, as evident in the PCA diagram. Nevertheless, differences among plot types were greater, as seen from the resulting sample groups in ordination space. Thus, the groups of plots are rather homogenous, which is important for formulating conclusions from the results. On the other hand, the conclusions are limited because no exact base-line data were available. The study plots were selected during the bark beetle attack and not before, because the attack was difficult to predict both in space and time.

The results were rather different for herbs and mosses. Whereas species composition of herbs did not differ very much between dead canopy and clearcuts in the first year, mosses, as sensitive organisms, responded to the salvage logging immediately, resulting in differences between dead canopy and clearcuts already in the first year. Waterlogged spruce forests, with only partly dead canopy and more moisture, seem to be more resistant to changes both in the herb and moss layers. Similarly Bauer (2002), who studied dead spruce forests after bark beetle outbreak in Bayerischer Wald, found only few changes in the herb vegetation after three years. Nevertheless, the important finding is that there were different trends of succession in clearcuts and under completely dead canopy after only five years. Clearcuts differed from the other plots by a sudden lack of a tree layer leading to a severe change in microclimatic conditions, which many forest species did not survive. Godefroid et al. (2005) noted that species such as *Dryopteris dilatata* and *Luzula sylvatica* are not able to survive a low level of air humidity in clearcuts. Pioneer species, such as *Juncus effusus*, *Agrostis capillaris*, *Chamaenerion angustifolium*, and *Taraxacum officinalis*, occurred in bare sites. All of these species are common in temperate hardwood forests after disturbances (Brunet et al., 1996). These species are characterized by having a persistent seed bank or effective dispersal by wind (Pykälä, 2004; Bauer, 2002). Therefore, soil disturbance caused by logging operations is important for their establishment; that is the reason they are not so common after a natural disturbance, such as bark beetle attacks. The same was found by Fischer (1992) and Fischer et al. (1990) when comparing cleared and uncleared windthrow areas. Forest species survived better in uncleared areas, where almost no soil disturbance occurred. On the contrary, disturbance of soil and vegetation by logging procedures led to

activation of the soil seed bank. Also, species possessing flying diaspores were able to invade similarly as in the present study.

A very slow process of regeneration of the original vegetation can be expected in clearcuts, together with the growth of a new tree layer. The regeneration time of forest ground layer vegetation depends on the type of forest, but mostly requires several decades. Godefroid et al. (2005) found a long-persistent effect of clearcutting on residual species. Seed sources (besides original species surviving after logging) and suitable microsites will be the most important factors for re-colonization of clearcuts by forest species in our study. The influence of microsites is often substantial in the case of species of conifer forests (Eriksson and Ehrlén, 1992). Consequently, the changed conditions, which are not suitable for forest species establishment, and strong grass competition can be considered as the greatest problems in clearcuts.

The disturbance caused by bark beetle appears to be very moderate compared to salvage logging: only partial needle loss occurred in the first year, while tree canopy became gradually more open in the following years due to continuing defoliation, breaking off of thin branches and later bigger branches and parts of trunks. These parts of dead trees fall, gradually decompose, and enrich the soil. Forest vegetation survived very well in such stands leaving pioneer species with almost no bare soil available for their establishment. Allen et al. (2006) reached similar conclusions in boreal forests of white (*Picea glauca*) and black spruce (*Picea mariana*) after a widespread outbreak of spruce beetles. They found a few changes in forest vegetation after five years since the outbreak and suspected that relatively few changes would occur in the cover or diversity of herbaceous species unless a significant ground disturbance occurred. The presumption that pioneer vegetation will not prevail in dead spruce forests after bark beetle outbreak is also supported by Jehl (2001). He found that pioneer species did not form a great part of the vegetation even 13 years after an extensive windstorm. Nevertheless, somewhat different results were obtained by Kupferschmid (2002) in Switzerland, where the vegetation changed due to invasion by *Rubus idaeus* shortly after the tree death due to bark beetle attack. For these reasons, permanent research plots are of great importance and their monitoring should continue. No comparable data are available in the case of waterlogged forests, which were supposed to be resistant to bark beetle attacks. Our results indicate that, although many trees in the waterlogged forests died, they are still relatively resistant to changes in the herb and moss layers, but the continuing observation of these permanent plots is very desirable.

Total covers of herb and moss layers and typical species

The severe effect of salvage logging is also reflected in the total cover of herbs. The greatest change of herb layer cover occurred in clearcuts: although the cover was the lowest here at the beginning, it increased so that it was the highest after five years, compared to the other plots. The greatest change in ground vegetation in clearcuts was probably not caused by changed light conditions due to missing canopy, because most forest vascular plants are resilient to changes in the canopy (Ewald, 2000). Direct mechanical disturbance of soil and vegetation was probably more influential. The herb layer cover increased slightly in waterlogged forests, but surprisingly, it remained unchanged under completely dead canopy of the mountain forests. Dead branches and parts of dead trees, gradually breaking off and falling down, are the factors obviously preventing expansion of grasses. The same phenomenon was described by Bauer (2002) from dead spruce forests in Bayerischer Wald. There was not so much litter material in waterlogged spruce forests, where many trees survived, so the effect of a more open canopy resulted in a slight increase of herb layer cover.

A different situation was found for mosses. Waterlogged spruce forests, with more than twice the cover of mosses at the beginning of the study compared to dead canopy, were very different from the other plots. From the beginning, the cover was the lowest in clearcuts, where mosses evidently did not survive the disturbance. An immediate drastic decline of moss cover was reported by Hannerz & Hånell (1997) after clearcutting and by Jalonen and Vanha-Majamaa (2001) even after single-tree selection system of felling. The moss layer cover did not increase even after five years in clearcuts in the present study. Some decrease of moss cover occurred under dead canopy and in waterlogged forests during the observation period, which is a common phenomenon under decreased tree layer cover (Vacek et al., 1999). Falling parts of branches and trees in dead stands, which prevent grass expansion and form a very structured terrain, can also be expected to preserve microsites with moist and shady microclimate suitable for mosses.

The cover of typical species in spruce forests, although different at the beginning, was similar in all plots after five years. Only two typical species, grass dominants *Calamagrostis villosa* and *Avenella flexuosa*, exhibited a rapid increase in clearcuts. Both species could fill open sites after logging. The situation was different under dead canopy, where *A. flexuosa* decreased because of competition with *C. villosa*. *C. villosa* also increased at the expense of *A. flexuosa* in forests influenced by acid deposition (Malcová et al., 1999). Similarly, Bauer (2002) found

decreased *A. flexuosa* cover after three years of observation of dead forests, but no change in the cover of *C. villosa*, which is in contrast to our findings.

Number of species

The number of herb species did not differ among plot types. The only significant increase occurred due to the establishment of some pioneer species in most plots. Bauer (2002) also found few changes in herb species numbers after three years in dead forests, where only a few new pioneer species occurred. These species established very slowly in a few cases. Therefore, rapid colonization of dead stands is not likely to occur in any case. Almost the same number of herb species was found by Jehl (2001) in an uncleared windthrow area.

The number of mosses decreased under dead canopy and in clearcuts, where it was the lowest. Similarly, Uotila and Kouki (2005) reported decreased number of liverwort species due to cuttings and management in boreal forests. The bark beetle in waterlogged forests had a different effect, because the number of mosses increased there. The reason can be that reduction in the tree canopy was not so high as to cause local extinction in the original species, although it created conditions for new species to establish.

The numbers of typical spruce forest species were the lowest, and did not increase over time in clearcuts. This is the best evidence showing the negative effect of salvage logging. Some studies document increased diversity after clearcutting in boreal forests (Pykälä, 2004). These forests naturally regenerate after large-scale destruction of the tree layer (mostly fire and uprooting), when the soil is disturbed and patches of bare soil occur (Bergeron et al., 2001). Many species are adapted to such conditions and hence clearcutting may lead to similar results. Nevertheless, natural disturbances in the studied mountain spruce forests seem to be different, without severe soil disturbance nor the species adapted to it. That can be the reason why we did not observe any pronounced increase in species number in clearcuts.

Reduced tree canopy caused by bark beetle attacks also seems to have a different effect on vegetation than that caused by crown damage due to air pollution. In stands damaged by air pollution, Vacek et al. (1999) found that the increased amount of light at ground level resulted in lower moss and herb richness over the course of the study. On the contrary, in our case the number of herb species slightly increased in all plots and the number of mosses even increased in waterlogged forests. This implies that vegetation response is site and disturbance specific (Pickett and White, 1985).

Life forms

The differences in covers of life forms reflected different conditions in the observed plots. Clearcuts differed from other plots by the increase in herb hemicryptophytes and the presence of moss therophytes (e.g. *Funaria hygrometrica*), which corresponds to re-colonization of bare sites by grasses and pioneer species. Salvage logging also logically led to the absence of moss epiphytes and the decrease of woody chamaephytes (*Vaccinium myrtillus*). Uotila and Kouki (2005) found a similar effect of management on boreal forest vegetation: grasses were more abundant in the managed boreal forest whereas chamaephytes were in the natural forests.

Ellenberg values

Evaluation of the Ellenberg indices showed the large influence of salvage logging especially on mosses. The mosses in clearcuts indicated a high pH value but low ones for moisture compared to other plots. The mosses also indicated a relatively high value of moisture under dead canopy compared to clearcuts. Thus, the conditions under dead canopy remain quite suitable for mosses.

Herbs differed from mosses in their moisture indication. These species indicated an even slightly higher value in clearcuts than under dead canopy. This can correspond to the situation in clearcuts where ground water table rises due to decreased transpiration of the tree layer (Pothier et al., 2003), but top soil layers can become drier. Herbs with deep roots can indicate more moisture and mosses with shallow rhizoids drier conditions.

Herb species preferring high levels of nitrogen and pH dominated under dead canopy. Hannerz and Hånell (1997) found species preferring high levels of nitrogen increased in the clearcut compared to shelterwood. It is evident that canopy reduction due to bark beetle will have a different effect on nitrogen than shelterwood. There are indications that defoliation caused by insect outbreaks can increase nitrogen availability by increased litter fall. The lower value of nitrogen in clearcuts could also be caused by increased leaching from clearcuts (Akselsson et al., 2004). Overall, mosses appeared to be more sensitive indicators of changing environmental conditions than herbs.

Conclusions

The results showed that natural disturbance, represented by bark beetle outbreak, had a different effect on vegetation than anthropogenic disturbance in the form of salvage logging. Most forest species survived quite well after bark beetle outbreak under dead canopy, with pioneer species rarely colonizing these areas. The smallest changes in vegetation were found in waterlogged forests. Forests affected by a large bark beetle outbreak and left without interventions most likely will not develop via a pioneer stage of succession in contrast to clearcuts. This conclusion is also supported by the natural regeneration of tree species in these plots (Jonášová and Prach, 2004). Grass species expanded in clearcuts formed due to salvage logging. Changes appeared in the moss layer composition, which were greatest in clearcuts, were more obvious than those of the herb layer. The development of clearcuts seems to be very different from the dead canopy plots. Our results indicate that no intervention in spruce forests attacked by bark beetle is a much better option for the restoration of these forests than any forestry measures. Further monitoring of permanent plots will be greatly needed. The moss layer should be especially observed in detail, because it is notably more sensitive to disturbances and subsequent environmental changes, and more species rich, than the herb layer in the mountain spruce forests.

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Appendix I. Mean covers of herb species per 400 m² plot in each type of plot and years. Covers lower than 1% are denoted by "+", the absence of a species is denoted by a dot.

	Dead canopy		Clearcut		Waterlogged	
	1997	2002	1997	2002	1998	2002
Typical species:						
<i>Avenella flexuosa</i>	26.0	15.0	16.9	26.5	2.8	6.5
<i>Calamagrostis villosa</i>	27.4	40.7	20.4	49.6	1.3	3.4
<i>Dryopteris dilatata</i>	2.1	2.5	+	+	+	+
<i>Homogyne alpina</i>	+	1.0	.	.	+	+
<i>Luzula sylvatica</i>	9.1	3.0	4.7	3.4	.	.
<i>Lycopodium annotinum</i>	+	+	1.0	+	+	+
<i>Oxalis acetosella</i>	+	2.9	+	+	+	+
<i>Trientalis europea</i>	+	1.5	+	.	+	+
<i>Vaccinium myrtillus</i>	14.2	10.0	1.5	2.0	25.3	30.0
<i>Vaccinium vitis-idea</i>	.	+	.	.	+	+
Other species:						
<i>Agrostis canina</i>	+	+
<i>Agrostis capillaris</i>	.	.	+	.	.	.
<i>Athyrium distentifolium</i>	+	+
<i>Bistorta major</i>	.	+
<i>Carex canescens</i>	.	.	+	2.5	+	1.1
<i>Carex echinata</i>	.	.	.	3.5	1.2	2.1
<i>Carex nigra</i>	+	+	.	.	+	+
<i>Chamenerion angustifolium</i>	+	+	+	+	.	+
<i>Deschampsia cespitosa</i>	.	.	.	+	.	+
<i>Epilobium montanum</i>	+
<i>Eriophorum vaginatum</i>	8.4	8.5
<i>Galium hircynicum</i>	+	1.3	+	+	.	+
<i>Hieracium</i> sp.	.	.	.	+	.	.
<i>Juncus effusus</i>	.	.	.	+	.	.
<i>Juncus filiformis</i>	.	.	.	+	+	.
<i>Juncus squarrosus</i>	.	.	.	+	.	.

<i>Maianthemum bifolium</i>	+	+	+	+	.	.
<i>Molinia coerulea</i>	5.0	5.6
<i>Nardus stricta</i>	+	+
<i>Polygonatum verticillatum</i>	+	+	+	.	.	.
<i>Prenanthes purpurea</i>	.	+
<i>Rubus idaeus</i>	+	+	+	1.3	.	+
<i>Rumex acetosella</i>	.	.	+	+	.	.
<i>Soldanella montana</i>	+	+	.	+	.	.
<i>Streptopus amplexifolius</i>	.	+
<i>Taraxacum officinale</i>	.	+	.	+	.	.

Appendix II. Mean covers of moss species per 400 m² plot in particular types of plots and years. Covers lower than 1% are denoted by "+", the absence of a species is denoted by a dot.

	Dead canopy		Clearcut		Waterlogged	
	1997	2002	1997	2002	1998	2002
Typical species:						
<i>Bazzania trilobata</i>	+	.	.	.	8.0	6.0
<i>Calypogeia azurea</i>	+	+
<i>Calypogeia integristipula</i>	+	+	.	.	+	+
<i>Dicranodontium denudatum</i>	+	+	+	+	5.3	3.3
<i>Dicranum scoparium</i>	3.8	2.2	3.6	1.2	3.7	5.0
<i>Lepidozia reptans</i>	+	+	+	+	4.1	2.0
<i>Lophozia lycopodioides</i>	+	+	+	+	+	+
<i>Polytrichastrum formosum</i>	9.7	5.0	4.2	1.9	4.7	6.8
<i>Polytrichum commune</i>	1.1	+	+	+	3.5	4.8
<i>Sphagnum girgensohnii</i>	2.7	1.8	+	.	5.0	5.0
<i>Tetraphis pellucida</i>	+	+	+	+	+	+

Other species:

<i>Anastrepta orcadensis</i>	+	+
<i>Bazzania tricenata</i>	+
<i>Blepharostoma trichophyllum</i>	+	.	.	+	.	+
<i>Calyptogeia neesiana</i>	+
<i>Cephalozia bicuspidata</i>	+	.	.	.	+	+
<i>Cephalozia leucantha</i>	+	.
<i>Cephalozia lunulifolia</i>	+	+	.	.	+	+
<i>Ceratodon purpureus</i>	.	.	+	.	.	.
<i>Chiloscyphus profundus</i>	+	+	.	.	.	+
<i>Dicranella heteromalla</i>	.	.	+	+	.	+
<i>Dicranum fuscescens</i>	1.6	+	2.2	.	+	1
<i>Dicranum montanum</i>	+	+	+	+	+	+
<i>Funaria hygrometrica</i>	.	.	+	+	.	.
<i>Herzogella seligeri</i>	+
<i>Hylocomium splendens</i>	+	.
<i>Hypnum cupressiforme</i>	+	+	+	+	+	+
<i>Jungermannia sphaerocarpa</i>	+
<i>Lophozia attenuata</i>	+	+	+	.	+	+
<i>Lophozia floerkei</i>	.	+	+	.	.	+
<i>Lophozia hatcheri</i>	+
<i>Lophozia longidens</i>	+	.
<i>Lophozia longiflora</i>	+	+	+	.	+	+
<i>Lophozia ventricosa</i>	+	+	+	+	+	+
<i>Marchantia polymorpha</i>	.	.	+	.	.	.
<i>Mylia anomala</i>	+	+
<i>Mylia taylorii</i>	.	.	.	+	+	+
<i>Oligotrichum hercynicum</i>	.	.	+	.	.	.
<i>Plagiothecium curvifolium</i>	+	+	+	+	.	+
<i>Plagiothecium denticulatum</i>	+	+
<i>Plagiothecium undulatum</i>	.	.	+	.	.	.
<i>Pohlia nutans</i>	+	.	+	.	.	+
<i>Polytrichastrum longisetum</i>	.	.	+	.	+	+

<i>Polytrichum juniperinum</i>	.	.	.	+	1.1	+	.
<i>Polytrichum strictum</i>	+
<i>Ptilidium ciliare</i>	+	+	.	.	.	+	+
<i>Ptilidium pulcherrimum</i>	+	+	+	+	+	+	+
<i>Ptilium crista-castrensis</i>	+	+
<i>Racomitrium microcarpon</i>	.	.	.	+	+	.	.
<i>Rhytidiadelphus loreus</i>	+	+	.	.	+	+	.
<i>Sanionia uncinata</i>	+	.
<i>Sphagnum capillifolium</i>	.	.	.	+	.	1.4	1.0
<i>Sphagnum denticulatum</i>	.	.	.	+	+	.	.
<i>Sphagnum fallax</i>	2.4	2.0
<i>Sphagnum magellanicum</i>	6.0	5.6
<i>Sphagnum palustre</i>	+	+
<i>Warnstorfia fluitans</i>	+

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Chapter V

Rehabilitation of monotonous exotic coniferous plantations: A case study of spontaneous establishment of different tree species

Jonášová, M. and Prach, K., 2006.
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Rehabilitation of monotonous exotic coniferous plantations: a case study of spontaneous establishment of different tree species

Abstract

Conversion of plantations of exotic coniferous species, such as Norway spruce (*Picea abies*), Douglas fir (*Pseudotsuga menziesii*), and Sitka spruce (*Picea sitchensis*), into more natural woodland is intended in two national parks in the province of Drenthe, The Netherlands. For that, artificial gaps in the plantations were made and natural regeneration of both indigenous and exotic species was investigated. A total of 87 sample plots were analysed, each 100 m² in size, and located under canopy or in the gaps. The densities of naturally established seedlings and saplings of tree species were recorded. Norway spruce attained the highest regeneration among all species investigated, both in gaps and under canopy. However, as in the case of other exotics (except Japanese larch, *Larix kaempferi*) its abundance was higher under canopy than in gaps. Indigenous species generally regenerated better in gaps than under canopy, forming 28% of the total number of seedlings in gaps and only 3.8% under canopy. The most numerous indigenous species were rowan (*Sorbus aucuparia*) and silver birch (*Betula pendula*). Scots pine (*Pinus sylvestris*) and pedunculate oak (*Quercus robur*) were less common. The most important factors influencing the regeneration of indigenous species were: numbers of seed trees within a 50m distance from the plot, the type of plot (gap or canopy), canopy cover, and age and size of gaps. It was obvious that regeneration of indigenous species can be stimulated by suitable forestry management practices, such as thinning dense stands and creating gaps of various sizes. Mixed stands of Norway spruce and indigenous broadleaves represent a reasonable target resulting from the interventions.

Key words: Natural regeneration; Forest management; Coniferous plantations; Gaps; Exotic species; Indigenous species; Seedlings.

Introduction

In temperate Europe, there are many extensive plantations of coniferous species on sites where mixed and broadleaf forests would otherwise prevail (Ellenberg, 1988). Decreasing public acceptance of monocultural timber plantations and increasing pressure from nature protection interests have encouraged conversion of plantations to more natural forest communities (Spiecker et al., 2004). Forest restoration generally cannot be seen as applying technical measures only (Buckley et al., 2002). Instead, methods using natural processes, such as natural regeneration of indigenous species, should be preferred in rehabilitation of forest ecosystems in a long-term perspective (Fanta, 1997; Diemont et al., 2006). The rationale for the shift from coniferous plantations back to mixed broadleaf forests has been recently discussed by many authors (e.g. Zerbe, 1994; Bouwma et al., 1997) as well as specific methods of conversion, including natural regeneration (Bode and Hohnhorst, 1994; Ratcliffe and Peterken, 1995; Kenk and Guehne, 2001). Natural regeneration has many advantages: in naturally regenerated woodland there is a greater diversity of structure and species than in planted forests, it often favours native species and generally encourages woodland conservation values. Finally, natural regeneration is usually cost-effective. The conservation benefits brought by using natural regeneration were outlined by Peterken (1981). There are indications that natural regeneration processes can be fairly successful under certain conditions, even in heavily managed plantations, and can act as a substitute for planting (e.g. Ackzell, 1994; Götz, 1994). The success of natural regeneration in coniferous plantations depends on many factors, both abiotic (light availability, microclimate, soil conditions) and biotic (sources of diaspores, seed dispersal agents, competition, browsing) (Malcolm et al., 2001). The most common problem in extensive plantations of exotic species seems to be a lack of seed trees of indigenous species. However, studies on seed dispersal of common European tree species indicate that even long-distance dispersal is possible (Stiles, 1992).

Usual problem in coniferous plantations, which can prevent some of the native species from successfully re-establishing, is low light intensity due to a dense canopy (Hale, 2001). Though many species can tolerate low light levels (a few per cent of full daylight) when seedlings, they usually demand more light for subsequent growth (Welander and Ottosson, 1998). On the other hand, overstorey cover also reduces the growth of herbaceous vegetation and consequently competition experienced by tree seedlings. Creating gaps of appropriate size has been reported as a suitable way for supporting natural regeneration of target

species (e.g. Dai, 1996; Coates, 2002; Diaci, 2002; Page and Cameron, 2006). The situation can differ site by site and species by species. The soil, especially the humus layer, and soil microorganisms were also reported to be important for tree regeneration (Elgersma, 1998). Ponge et al. (1998) summarised the various aspects into an integrated view of forest regeneration processes.

The transformation of coniferous plantations into semi-natural woodlands is a generally recognised problem in the province of Drenthe in The Netherlands, where extensive Norway spruce plantations exist in the area of national parks Dwingelderveld and Drents-Friese Wold. Most stands are first generation monocultures planted on earlier heathlands. The main objective of contemporary forestry in this region is to increase the proportion of indigenous broadleaved trees and to convert pure coniferous stands into mixed stands (van de Bos, 2002).

This study evaluates the possibility of natural regeneration in coniferous forest stands after forestry interventions aimed to rehabilitate the plantations. It aims to particularly answer the following questions: Do forestry management practices, such as thinning dense stands and creating gaps of various size, support natural regeneration especially of indigenous species? What are the most important factors supporting or limiting natural regeneration of particular tree species?

Methods

Study area

The study area includes the coniferous stands of the forest management units Dwingeloo (6°25'E, 52°49'N) and Smilde (6°21'E, 52°53'N), situated in the southwestern part of Drenthe province in The Netherlands. The area belongs to the Northern Temperate Zone, having a maritime climate characterised by mean annual temperature about 8.6°C, precipitation varying between 915 and 975 mm and relatively low evaporation during the growing season. The altitude of the study area is between 11 and 12 m above sea level. Humus podsol is the prevailing soil type. Ground water level is usually in the range of 30 – 200 cm (Vrieling et al., 1976; Meklink and Kleijer, 1985).

The prevailing potential natural vegetation is the beech-oak forest (*Fago-Quercetum*) on the more productive sites and the birch-oak forest (*Betulo-Quercetum*) on dry and nutrient poor sandy sites (van der Werf, 1991). Common tree and shrub species in these natural forests are *Fagus sylvatica*, *Quercus robur*, *Betula pendula*, *B. pubescens*, *Pinus sylvestris*, and *Sorbus aucuparia* (Dirkse, 1993).

Parts of the management units Dwingeloo and Smilde were dominated by drift sand at the beginning of the 20th century. In that time, new forests were planted, using predominantly Scots pine, to stabilise the drift sand and to protect the surrounding agricultural land from wind erosion. The plantations of exotic coniferous species were started in the 1920s and 1930s, primarily in areas between the drift sand where the soil was richer in nutrients and water. The main species used were Norway spruce (*Picea abies* (L.) Karst.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Sitka spruce (*Picea sitchensis* Carr.), all of which have been found to grow well with high yields on these sites.

Gaps of different sizes have been made by forestry authorities in the last ten years to give a more irregular structure to the plantations and to support the establishment of 'desirable' or target indigenous species. The gaps and clearings were created in homogenous stands. Only trees were removed without any intentional disturbance of the herb layer. Mature trees of indigenous species, such as birch (*Betula pendula* Roth), rowan (*Sorbus aucuparia* L.), Scots pine (*Pinus sylvestris* L.), pedunculate oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) were the only sources of diaspores occasionally occurring as single trees in the plantations, more often as a few trees on the borders of the plantations.

Field sampling

A total of 87 sample plots were established, each 100 m² in size, in available stands of Norway spruce (71 plots), Sitka spruce (6 plots) and Douglas fir (10 plots). Two types of plots were compared: 42 plots in gaps and clearings of various size (diameters 10 – 120 m), and 45 plots located under canopy, in the nearest, sufficiently large undisturbed stands. Sample plots were always located in the centre of a clearing or a close stand.

The following parameters were recorded for each sample plot in 1999:

- spontaneously established seedlings and saplings of all species, they were separated into two categories according their height: Category 1 up to 0.5 m, Category 2 above 0.5 m
- numbers of seed trees in the surroundings of the sample plot within a distance of 50 m from the center of the plot; the arbitrary scale was defined as follows: 0 = no seed trees, 1 = 1-10 seed trees, 2 = 11-50 seed trees, 3 = 51-100 seed trees, 4 > 100 seed trees
- the type of plantation (Norway spruce, Sitka spruce, Douglas fir)
- the thickness of the humus layer (in cm)
- the type of ground layer and its coverage (%): herb layer, mosses, litter

Parameters recorded only in gaps:

- age of the gap (1 - 10 years)
- size of the gap (scale for the radius of the gap: 1 < 10 m, 2 = 10-20 m, 3 = 21-30 m, 4 = 31-40 m, 5 = 41-50 m, 6 > 50 m)

Parameters recorded only in close stands:

- age of the stand (35 – 70 years)
- crown canopy (40 – 70 %)

Statistics

Numbers of seedlings for a particular species were compared in the types of plots (i.e. gaps vs. canopy) using t-test for independent samples. In the next step the influence of a number of explanatory variables was identified for each particular species by a regression model. Separate analyses were made for plots in gaps and those under canopy, including parameters recorded only in gaps (age, size) or under canopy (age, canopy cover). Although there are several ways how to select factors significantly influencing natural regeneration of particular species, we used stepwise regression analyses as the most convenient. Analyses were performed with the Statistica programme (Statsoft, 1999).

The numbers of seedlings (both indigenous and exotic) together with the environmental variables recorded both in gaps and under canopy were evaluated using Canonical Correspondence Analysis (CCA) in the Canoco programme (Ter Braak and Šmilauer, 1998). The numbers of seedlings in two height categories were used as response data. The explanatory variables were combined into groups of variables, i.e. the group 'Seed Trees' includes the numbers of seed trees of all particular species, the group 'Management' includes gap size, gap age, canopy and stand age, the group 'Ground layers' includes covers of mosses, herb layer and litter, and thickness of humus layer. Particular analysis was made for each group of explanatory variables and the variability explained by each group was determined. Monte Carlo permutation test was used to test the significance of canonical axes. Then a global analysis was made, where all explanatory variables were used together and tested by Monte Carlo permutation test to select the variables with significant influence on the response data. The criteria for a variable to be included were set at $p \leq 0.05$. The resulting ordination diagram was produced by the CanoDraw programme (Ter Braak and Šmilauer, 1998).

Results

Species composition of natural regeneration

The plots varied markedly in the numbers of seedlings of particular species. The seedlings of 4 indigenous and 7 exotic tree species were recorded (Table 1). Norway spruce was the most common regenerating species, both in gaps (in 68.3% of all samples) and under canopy (89.1% of all samples). Rowan was the most frequently occurring indigenous species, being recorded in 80.4 % of all samples under canopy and in 61% of gaps. Among all recorded seedlings and saplings, the proportion of all indigenous species together was only 3.7% under canopy but 27.8% in gaps.

Table 1. Presence of seedlings of all species in gaps and under canopy.

Species	Average seedlings density per ha recorded *		Percentage of plots where the species was present		Percentage of species in the whole regeneration	
	gaps	canopy	gaps	cano-py	gaps	cano-py
Natives						
Silver birch (<i>Betula pendula</i> Roth)	1,250 (867)	50 (0)	65.9	15.2	10.7	0.1
Rowan (<i>Sorbus aucuparia</i> L.)	1,260 (691)	1,000 (128)	61	80.4	10.8	2.8
Pedunculate oak (<i>Quercus robur</i> L.)	200 (16)	140 (0)	56.1	50	1.7	0.4
Scots pine (<i>Pinus sylvestris</i> L.)	530 (162)	150 (0)	51.2	13	4.6	0.4
Exotics **						
Norway spruce (<i>Picea abies</i> (L.) Karst.)	7,470 (3,124)	32,760 (2.2)	68.3	89.1	63.8	89.9
Sitka spruce (<i>Picea sitchensis</i> Carr.)	140 (69)	1,640 (0)	9.8	6.5	1.2	4.5
Douglas fir (<i>Pseudotsuga menziesii</i> (Mirb.) Franco)	250 (164)	410 (0)	39	34.8	2.1	1.1
Japanese larch (<i>Larix kaempferi</i> Carr.)	530 (333)	180 (6.5)	41.5	26.1	4.6	0.5

* Total numbers and numbers of saplings taller than 50 cm (in parentheses)

** Only occasionally seedlings of Red oak (*Quercus rubra* L.), White pine (*Pinus strobus* L.), and Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were found.

The average number of Norway spruce under canopy (328 seedlings per 100 m²), was significantly higher than in gaps where 75 seedlings per 100 m² were recorded (t-test: t-value = -2.98, p = 0.004). Scots pine and birch seedlings had a clear preference for gaps (Scots pine: t-value = 4.09, p < 10⁻⁴, birch: t-value = 5.98, p < 10⁻⁶). No significant differences between gaps and canopy were found in the case of other species and no indigenous species was seen to prefer growing under canopy.

Comparing the total numbers of seedlings and saplings with those of saplings taller than 50 cm we can see that the species survived much better in gaps than under canopy. Under canopy, the taller saplings of only three species were recorded (Table 1).

Factors influencing natural regeneration

Relationships between the total numbers of seedlings of each indigenous and exotic species and environmental factors, analysed with stepwise regression, are presented in Table 2. The only factor significant for regeneration of all species was the number of seed trees within 50 m. Forest management indicators (crown canopy cover, gap size, gap age and stand age) were significantly correlated to seedling establishment of some species. Gap size was significant for birch (preference for larger gaps) and Japanese larch (preference for smaller gaps), while the age of the gap was correlated with the number of seedlings of pedunculate oak, spruce and Douglas fir (more seedlings in older gaps). The second most important factor under canopy (beside seed trees) was the canopy cover, which had a significant negative effect on the regeneration of pedunculate oak, rowan and spruce. The influence of stand age was found only for larch, which preferred stands of lower age. The character of ground layer was significant in several cases: mosses influenced positively the number of spruce and oak seedlings, and herb layer influenced negatively the number of rowan seedlings in gaps. The influence of humus layer thickness was significant only in the case of larch under canopy and no significant influence of litter coverage on natural regeneration was found. From the values of the standardised regression coefficients it is obvious that numbers of seed trees can explain more variability in the numbers of seedlings than management and the character of ground layer.

Table 2. Stepwise regression analyses of numbers of naturally regenerating seedlings.

<i>Sorbus aucuparia</i> in gap			<i>Sorbus aucuparia</i> under canopy		
R ² = 0.25, F = 7.17, p < 0.002			R ² = 0.40, F = 14.10, p = 0.00002		
Parameter estimate	Beta	B	Parameter estimate	Beta	B
Intercept	-	0.73	Intercept	-	1.42
Rowan	0.44	0.57	Rowan	0.5	0.61
Herb layer	-0.3	-0.0072	Canopy cover	-0.28	-0.02

<i>Quercus robur</i> in gap			<i>Quercus robur</i> under canopy		
R ² = 0.29, F = 5.65, p = 0.0025			R ² = 0.31, F = 9.69, p < 0.0003		
Parameter estimate	Beta	B	Parameter estimate	Beta	B
Intercept	-	n.s.	Intercept	-	0.62
Oak	0.53	0.31	Oak	0.49	0.25
Mosses	0.28	0.0035	Canopy cover	-0.28	-0.01
Gap age	0.14	0.011			

<i>Betula pendula</i> in gap*			<i>Pinus sylvestris</i> in gap*		
R ² = 0.59, F = 27.50, p < 10 ⁻⁶			R ² = 0.36, F = 11.66, p < 0.0001		
Parameter estimate	Beta	B	Parameter estimate	Beta	B
Intercept	-	0.3	Intercept	-	0.23
Birch	0.53	0.83	Pine	1.6	0.95
Gap size	0.28	0.2			

<i>Picea abies</i> in gap			<i>Picea abies</i> under canopy		
R ² = 0.51, F = 14.47, p = 10 ⁻⁶			R ² = 0.39, F = 13.95, p = 0.00002		
Parameter estimate	Beta	B	Parameter estimate	Beta	B
Intercept	-	n.s.	Intercept	-	1.19
Spruce	0.31	0.24	Spruce	0.55	0.51
Mosses	0.34	0.01	Canopy cover	-0.2	-0.02
Gap age	0.3	0.06			

<i>Picea sitchensis</i> in gap			<i>Picea sitchensis</i> under canopy		
R ² = 0.69, F = 46.14, p < 10 ⁻⁶			R ² = 0.66, F = 42.27, p < 10 ⁻⁶		
Parameter estimate	Beta	B	Parameter estimate	Beta	B
Intercept	-	n.s.	Intercept	-	n.s.
Sitka	2.2	0.94	Sitka	2.17	2.3

<i>Pseudotsuga menziesii</i> in gap			<i>Pseudotsuga menziesii</i> under canopy		
R ² = 0.37, F = 12.08, p = 0.00007			R ² = 0.59, F = 30.90, p < 10 ⁻⁶		
Parameter estimate	Beta	B	Parameter estimate	Beta	B
Intercept	-	n.s.	Intercept	-	n.s.
Douglas	0.61	0.26	Douglas	1.6	0.71
Gap age	0.28	0.03			

<i>Larix kaempferi</i> in gap			<i>Larix kaempferi</i> under canopy		
R ² = 0.46, F = 18.15, p < 10 ⁻⁵			R ² = 0.38, F = 8.44, p = 0.0002		
Parameter estimate	Beta	B	Parameter estimate	Beta	B
Intercept	-	0.69	Intercept	-	0.4
Larch	0.63	0.45	Larch	0.44	0.19
Gap size	-0.12	-0.21	Humus	0.26	0.0022
			Stand age	-0.29	-0.0085

Criterion for a variable to be included in the model was set to $p \leq 0.05$. The common names of trees among variables indicate seed trees of the particular species. Beta = standardised regression coefficient, B = non-standardised regression coefficient.

* *Betula pendula* and *Pinus sylvestris* did not exhibit any significant relationships under the canopy.

From the summarized results of CCA analysis (Table 3) it is also obvious that the number of seed trees in the vicinity of a plot can explain a significant part of the variability in the species data (35.7%). Management interventions and ground layers explained 21.2% and 15.4%, respectively. After including the other groups of variables as covariables, seed trees explained again the greatest part of

variability (24.6%) and management explained 9.1%. The effect of ground layer, i.e. thickness of humus layer, and herb, moss and litter coverage, were not significant after including seed trees and management as covariables.

In the results of CCA analysis (Fig.1) there is evident that saplings of all species above 50 cm tended to prefer gaps, while small seedlings, except light-demanding birch and pine, are more related to canopy. Both height categories of birch and pine prevailed in gaps. Among indigenous species, rowan seems to be the most connected to canopy. Small seedlings of exotic species unambiguously preferred canopy, except Japanese larch, which did not have a clear preference. However, tall seedlings of exotics were related to gaps. Gap age had a positive influence especially on high seedlings of Sitka spruce, oak, birch and Norway spruce.

Table 3. Results of CCA analysis. The second column shows percentage of the total variation in species data that can be explained by each group of factors without including the others. In the third column, there is the pure variability explained by each group, which cannot be accounted for by the other group (computed after including the other group as covariables).

Group of environmental variables	Max. expl. variability (%)	Pure variability (%)	Included variables
Seed trees up to 50 m distance	35.7	24.6	Numbers of seed trees of all species
Management	21.2	9.1	Gap age, gap size, canopy cover, stand age
Ground layer and humus	15.4	n.s.	Cover of herb layer, cover of mosses, of litter, thickness of humus layer
Total explained variability (%)		47.0	Numbers of seed trees, canopy, gap age, gap size

Norway spruce and Douglas fir seed trees had generally highest influence on the number of seedlings, while rowan had not any (see the length of arrows in Fig. 1). The relations to their own seed trees exhibited small seedlings of all conifers. The type of plantation (Norway spruce, Sitka spruce, Douglas fir) was,

naturally, strongly correlated with the number of seed trees of the respective species and therefore not considered in this analysis.

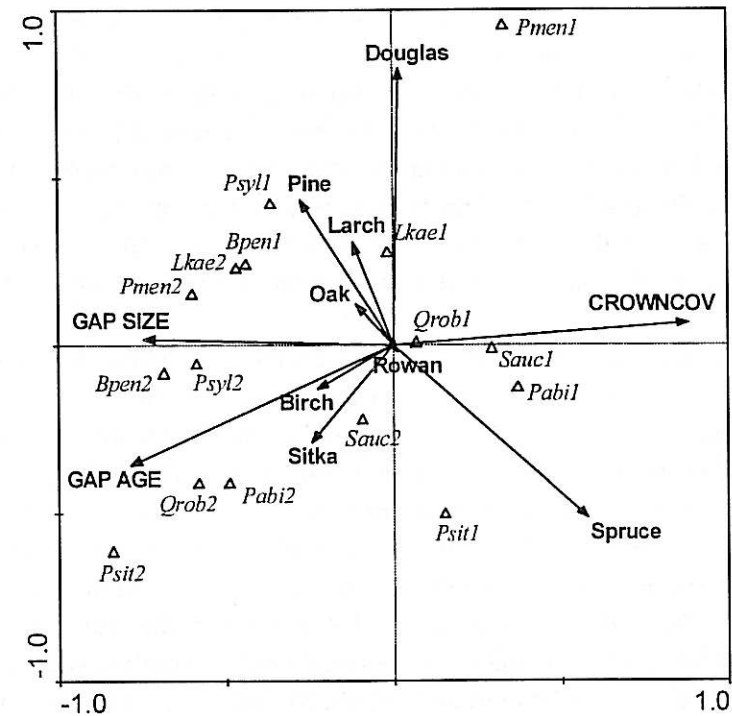


Fig. 1. CCA analysis showing numbers of seedlings divided into two high categories (in italics) in relation to the occurrence of seed trees (common names, in bold) and type of plot (canopy, gap). All canonical axes together explained 47% of the total variability in the species data (see Table 3). Abbreviations of species names: Betpen – *Betula pendula*, Pinsyl – *Pinus sylvestris*, Sorauc – *Sorbus aucuparia*, Querob – *Quercus robur*, Larkae – *Larix kaempferi*, Picabi – *Picea abies*, Picsit – *Picea sitchensis*, Psemen – *Pseudotsuga menziesii*.

Species indicated with 1 = individuals ≤ 50 cm, species indicated with 2 = individuals > 50 cm.

Discussion

The results of this study demonstrate that seed sources and silvicultural interventions are important factors, which determine both quantity and quality of natural regeneration and thus future forest composition. Regarding the total number of seedlings of individual species, Norway spruce was the predominant species. This dominance was evidently a consequence of the fact that the majority of study plots were located in Norway spruce-dominated stands where an abundant and frequent seed rain can be expected. Norway spruce, similarly as other exotics Douglas fir and Sitka spruce, regenerated better under canopy than in gaps, meanwhile the opposite was true for most indigenous species, except rowan. However, the subsequent seedling growth was better in gaps in the case of all species.

Rowan was the next most common species after Norway spruce and the occurrence of other indigenous species, namely birch, pedunculate oak, and Scots pine, was also promising for rehabilitation of the plantations, regarding the numbers of seedlings. Rowan represents a special case. Its seedlings, in contrast to all other species, were also found in many plots where no seed trees were recorded. This indicates that rowan has the capability for long distance dispersal greater than the arbitrarily considered 50 m. Leder (1997) found the distance of rowan seed trees to be a decisive factor regulating the amount of natural regeneration. He found the maximum regeneration to occur between 1 and 50 m away from seed trees, the minimum between 51 and 200 m and a second peak of seedling numbers between 301 and 350 m distance from seed trees. This bimodal pattern can be attributed to the activity of birds in that many species void their intestines this far into their flight (Kollmann, 1994; Leder, 1997). Great ability of rowan to colonize disturbed Norway spruce forests is well-known in Central Europe (Moravčík, 1994; Jonášová and Prach, 2004). Thus, we can assume its increase with increasing intensity of canopy thinning.

Oak seed trees were rather common in the study area, while their seedlings generally occurred in low numbers. Oak, whose seed trees were found in the vicinity of almost 65 % of the sample plots, is not considered to be limited by seed dispersal within this distance (Bossema, 1979; Jensen and Nielsen, 1986). Probably rather specialised site conditions required by the species, lower seed production, and especially seed consumption can play a role (Crawley and Long, 1995).

Birch and Scots pine, the most light-demanding species, were found predominantly in gaps. Moreover, birch preferred large gaps, which will be

obviously related to the way of its seed dispersal by wind within long distances (Perala and Alm, 1990). Birch was reported to colonize close conifer stands within 100 m of seed sources (Patterson, 1993).

No seedlings of beech (*Fagus sylvatica*), another important indigenous species potentially occurring in the area (Dirkse, 1993), were recorded. No mature beech tree was found within 50 m distance from the plots, although mature trees are scattered over the area. There is sufficient evidence that small rodents as bank vole (*Chlesterionomys glareolus*) and wood mice (*Apodemus sylvaticus*) are important for its seed dispersal (Jensen, 1985). Nevertheless, their dispersal distance is limited to a distance between 10 to 20m, only exceptionally up to 80m (Den Ouden, 2000). Thus, the absence of beech seedlings in our study could be attributed to insufficient source and dispersal of beechnuts over the studied area.

The other factors influencing, beside seed sources, natural regeneration include some forest management interventions. The differences in species regeneration in gaps and under canopy were obvious. Oak, as probably the most important target species in the area (Dirkse, 1993), has an intermediate demand for light (Lyr et al., 1992). Successful regeneration of oak under thinned coniferous stands was reported by Götmark et al. (2005), but according to Welander and Ottosson (1998) oak is able to regenerate even under a dense canopy. In our area, it was preferably found either in thinned stands (with crown canopy at about 40 – 50%, data not presented here) or in older gaps, i.e., in gaps already colonised by pioneer species. The ecological characteristics of oak indicate that there should be no problem in supporting its regeneration through forestry interventions, i.e. opening the canopy through thinning and gap formation, if under the absence of seed trees in combination with artificial sowing or planting. Gaps also provide better conditions for the regeneration of shade-intolerant, early successional species such as birch and Scots pine (Lyr et al., 1992; Verwijst, 1998), which were able to successfully establish and grow almost exclusively in gaps.

Seedlings and saplings up to 50 cm of Norway and Sitka spruce, and Douglas fir appeared to be shade tolerant and clearly preferred canopy for its regeneration. But they need more light for successful growth. A slight increase in light levels under canopy may strongly increase regeneration of Norway spruce (Leemans, 1991). Gaps are successfully used to promote spontaneous regeneration of Sitka spruce in its plantations (Hale, 2001; Page and Cameron, 2006). Thus, management measures to promote the regeneration of indigenous species by increasing light availability (creating gaps, thinning) also promotes the regeneration of the exotic species. Although light conditions were not directly

measured, they can be effectively substituted by estimating the canopy cover (Shugart, 1984) as applied in this study.

It seems, seed dispersal is the crucial difference between indigenous and exotic species regeneration ability. The exotic coniferous species present in the study area can probably neither be dispersed over long distances by birds, like oak and rowan, nor by wind like the light anemochorous seeds of birch. Mair (1973) reported the majority of seeds for Sitka spruce and Douglas fir falling within a distance of one or two tree heights. Thus, regeneration of these species is restricted to the vicinity of the seed trees that means it is feasible in plantations of the species and in their close surroundings. Moreover, there is no evidence of a seed bank of viable seeds of these coniferous species in the soil (Nixon and Worrell, 1999). If the seed trees of the exotic species are gradually removed (starting with the removal of the most vital seed bearing trees), these species cannot be expected to regenerate significantly at a distance greater than 50 m. Adopting this strategy might reduce the probability of the expansion of these exotic species.

Implications for practice

The results of this study confirm that allowing spontaneous regeneration is a reasonable and promising way of transforming monotonous coniferous plantations into more diverse stands with a higher participation of target indigenous tree species. Their natural regeneration can be supported in the studied area very effectively by management interventions, i.e. by thinning of the canopy and making gaps, although the same also promote regeneration especially of Norway spruce, the dominant exotic species. Its future selective cutting in gaps is recommended to decrease its competitive influence (shading) on the indigenous species. A target represented by mixed spruce-broadleaves forests can be realistically reached in the next several decades. The idea to eliminate completely the exotic species in favour of only indigenous broadleaf trees in a reasonable time is not very realistic under present circumstances. To verify the conclusions, it would be desirable to repeat the analyses in later stages of the gaps development. We assume, the same strategy should be applied in other areas where similar extensive plantations of these exotic conifers prevail.

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CHAPTER V

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Chapter VI

Summary of results and general conclusions

Summary of results and general conclusions

Mountain spruce forests influenced by bark beetle outbreak: the results of non-interventional approach

Natural regeneration

The results showed ongoing regeneration processes in the forests affected by bark beetle outbreak. The natural regeneration of trees was composed almost entirely of original species of mountain spruce forests, i.e. spruce (*Picea abies*) and rowan (*Sorbus aucuparia*), both under dead and partly surviving canopy. Beech (*Fagus sylvatica*), birch (*Betula pubescens*) and willow (*Salix* sp.) were rarely found. Spruce regeneration was the greatest in all plots, consisting of thousands of seedlings per ha. These numbers were several times higher than in clearcuts and sanitation stands. The second most numerous species was rowan, which had hundreds of seedlings per ha. Rowan was especially abundant under completely dead canopy, where their numbers increased several times during the observation period. There was a positive effect of open canopy on seedling growth under dead canopy as well as a protective effect of fallen stems and branches against browsing.

Microhabitat preferences were identified for spruce seedlings; regeneration of broadleaved species was found not to be dependent on the type of microhabitat. Dead wood was found to be the most favorable microhabitat for spruce seedlings. Other favorable microhabitats were spruce litter and mosses. Shading by snags seems to be an important factor under dead canopy, in moderating the changes caused by canopy reduction.

Ground layer

Most herb and moss species both survived quite well after bark beetle outbreak under dead canopy, with pioneer species sparsely occurring. Typical species of mountain spruce forests, such as *Lycopodium annotinum*, *Dryopteris dilatata*, *Homogyne alpina*, *Oxalis acetosella*, and *Soldanella montana*, survived under dead canopy. The continued dominance of *Vaccinium myrtillus*, along with an abundant moss layer, indicated that minimal vegetation changes occurred under partly dead canopy of waterlogged forests.

Mean numbers of herb species did not differ among the observed types of plots. The numbers of mosses and typical species of mountain spruce forests (herbs and mosses together) were significantly lower in clearcuts compared to non-interventional stands.

The influence of interventions against bark beetle outbreak

Natural regeneration

The effects of two types of interventions, salvage logging and sanitation, were evaluated. Both types of intervention against bark beetle caused large reductions in spruce regeneration compared to non-interventional stands. The numbers of both spruce and rowan were lower in the clear-cuts than under the dead canopy, and moreover, their height and age structure were reduced. Almost all of the youngest age-category spruce seedlings, originally the most numerous, were destroyed by cutting interventions against bark beetle or died soon after cutting due to the severe change of environmental conditions. Although the sanitation intervention was proposed by forest management as being close to nature, its results were largely different compared to natural disturbances and, regarding spruce regeneration, only slightly better than clearcutting. However, sanitation plots were evaluated only by a single observation, and continued monitoring will be needed to obtain more precise results.

The number of rowan stagnated after an initial increase to about one hundred seedlings per ha in clearcuts. Although rowan is considered to be a pioneer species, its numbers in clearcuts were lower than under canopy, evidently due to problems with its spread by birds in treeless sites and browsing. All wind-dispersed pioneer species (*Salix* sp. div., *Betula* sp. div. and *Populus tremula*) were almost entirely found in plots without canopy, which their numbers being much higher in clear-cuts (several hundreds) than in sanitation plots.

The extent of favorable microhabitats for spruce in clearcuts decreased while that of unfavorable ones, i.e. especially herb layer, increased. The most severe change occurred with wood removal, resulting in the loss of potential microhabitats for spruce seedling establishment. The sanitation plots were covered by large amounts of debarked logs, which can be a suitable microhabitat for seedlings only after they decay. This process will probably last several decades.

Ground layer

Typical species of mountain spruce forests decreased, being partly replaced by pioneer species, such as *Rubus idaeus*, graminoids *Calamagrostis villosa*, *Avenella flexuosa* and *Luzula sylvatica*, and in strongly waterlogged sites also by *Carex canescens* and *C. echinata*, i.e. species unfavorable for spruce regeneration. The most obvious changes appeared in the species composition of the moss layer, which was largely changed in clearcuts. The large increase in grass species cover may lead to the formation of a long-lasting and stable successional phase with the dominant grass vegetation hindering tree seedling establishment and development of a new forest.

Possibilities of natural regeneration of native trees in coniferous plantations

The results showed that forest management measures, i.e. thinning of the canopy and making gaps, can effectively influence the composition of natural regeneration in coniferous plantations. The presence of native tree seed sources in the neighboring areas around plantations was identified as an important factor influencing natural regeneration of all particular species. This must be considered in the process of transformation of these plantations. Norway spruce was the most numerous species naturally regenerating, due to abundant seed sources, although the indigenous species rowan (*Sorbus aucuparia*), oak (*Quercus robur*), birch (*Betula pendula*), and Scots pine (*Pinus sylvestris*) formed a substantial part of this regeneration. Gaps provided better conditions for the regeneration of shade-intolerant, early successional species, such as birch and Scots pine. Norway spruce, similarly as the other exotic species Douglas fir (*Pseudotsuga menziesii*) and Sitka spruce (*Picea sitchensis*), regenerated better under canopy than in gaps. However, the opposite was true for most indigenous species, except rowan, which slightly preferred canopy to gaps. Rowan was the best spreading species in the plantations, being found, in contrast to all other species, in many plots where no seed trees were recorded. However, subsequent seedling growth was better in gaps for all species.

General conclusions

Disturbances were shown to be the key factor conditioning the natural regeneration of both studied forest ecosystems: mountain spruce forests and artificial plantations. Bark beetle supports natural regeneration not only in strictly natural spruce forests, as has already been documented many times, but also in the previously managed mountain spruce forests. This is indicated by the fact that most species appeared to be adapted to the disturbance caused by bark beetle, and survived in attacked forests. The protective function of dead canopy and slow decay of dead trees are probably the most important attributes of this type of disturbance. Due to gradually falling dead trees, the monotonous terrain with a minimum of dead wood is replaced by a broken terrain with many different microhabitats. In place of the originally homogenous stands, the formation of new forest with a natural clump structure can be expected. Consequently, bark beetle can be seen as not only the means of spruce forest regeneration, but also the means of restoring their natural character. In contrast to natural disturbance, mountain spruce forests appeared to be very sensitive to artificial disturbance resulting from interventions against bark beetle. Their effects were only negative and, except for commercial stands, they should be excluded.

In coniferous plantations, artificial disturbance can simulate natural disturbance, which cannot be expected, especially in young plantations. The similar effect of these disturbances in both types of spruce stands is indicated by the similar occurrence of rowan and birch. Rowan preferred dead canopy and, thus, thinned canopy in plantations. Birch preferably regenerated in clearcuts and gaps. Since spruce plantations are grown mostly in different climatic conditions compared to mountain spruce forests, artificial disturbances do not seem to have the same negative effects as in mountain spruce forests and can be recommended as a tool for plantation transformation.

ERRATUM

Natural Regeneration and Vegetation Changes
in Disturbed Norway Spruce Forests

Magda Jonášová

PhD. thesis

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