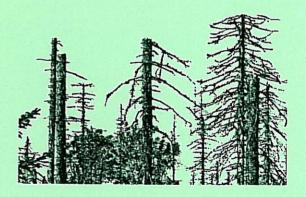
Faculty of Biological Sciences University of South Bohemia České Budějovice, Czech Republic



Summary of PhD. thesis

Natural Regeneration and Vegetation Changes in Disturbed Norway Spruce Forests

Magda Jonášová



supervisor prof. RNDr. Karel Prach, CSc.

> České Budějovice 2006

This research was supported by grants MSM/1231/0004 and AVOZ 6005908, and the fellowship of The Netherlands Ministry of Agriculture, Nature Management and Fisheries.

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; Pontailler 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 largescale 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 back 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 Sumava 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 sylavtica) 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

pubercens) 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 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.

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Contents

The thesis is composed of four original studies:

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

Jonášová, M. and Prach, K., 2004. Ecological Engineering 23: 15-27

Abstract: In the 1990s, a bark beetle (*Ips typographus*) outbreak caused a dieback of semi-natural mountain spruce (*Picea abies*) forests in the Sumava 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 tylvatica*). In clear-cut areas, the

numbers of spruce and rowan were significantly lower than under the dead canopy. Pioneer species such as willow (Salix aurita), birch (Betula pubescens), and aspen (Populus tremula) appeared in the clear-cut areas. The dependence of spruce regeneration on the availability of suitable microhabitats was found: decaying wood and spruce litter was found as the most favourable. The results confirmed that the original tree species of the mountain spruce forests regenerate well under dead canopy. The bark beetle outbreak does not result in the complete loss of the forests and could even be considered as a tool for the restoration of their natural character.

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

Jonášová, M. and Matějková, I. [manuscript]

Abstract: An extensive area of mountain spruce (Picea abies (L.) Karst.) forests, including waterlogged forests, in the Sumava 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 severe destruction of forests, being followed by formation of pioneer stages with a postponed spruce regeneration. In sanitation stands, the reduction of both previous vegetation and tree regeneration was obvious. Both interventions against bark beetle significantly led to severe disturbance of the whole ecosystem and considerably delayed restoration of these forests.

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

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

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.

4. Rehabilitation of monotonous exotic coniferous plantations: A case study of spontaneous establishment of different tree species Jonášová, M., van Hees, A. and Prach, K. Ecological Engineering 28: 141-148

Abstract: Conversion of plantations of exotic coniferous species, such as Norway spruce (Picca 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 purpose, 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 100m2 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 kaempfen), 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 forestrymanagement practices, such as thinning

Summary of results

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

dense stands and creating gaps of various sizes. Mixed stands of Norway spruce and indigenous

broadleaves represent a reasonable target resulting from the interventions.

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 (Pieea abies) and rowan (Sorbus aucuparia), both under dead and partly surviving canopy. Beech (Fagus pylvatica), 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, Drypteris 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 trenula) were almost entirely found in plots without canopy, whith 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 aucaparia), 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 (Pieca sitchensii), 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.

Mgr. Magda Jonášová

Born: July 2, 1973 in Vimperk, Czech Republic

Education

1996: MSc. – Charles University, Prague – Environmental conservation, graduated with the thesis "The influence of long-term stress on the assimilation structures of Norway spruce in the Šumava Mts".

1997 – present: PhD study – Department of Botany, University of South Bohemia, České Budějovice, thesis "Natural regeneration and vegetation changes in disturbed Norway spruce forests".

Professional appointments

2000 – 2003: Lecturer, Department of Biology, Pedagogical faculty, University of South Bohemia, České Budějovice

2003 – present: Research assistant, Laboratory of Forest Ecology, Institute of Landscape Ecology (now Institute of Systems Biology and Ecology), Czech Academy of Sciences, České Budějovice 2004: Research assistant, Insitute of Botany, Czech Academy of Sciences, Třeboň.

Research-stay abroad

1999: The Netherlands, Instituut voor Bos- en Natuuronderzoek (IBN-DLO, now Alterra) in Wageningen, focused on spruce plantations and posibilities of their tranformation (4 months)

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