Natural regeneration and vegetation changes in wet spruce forests after natural and artificial disturbances

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Abstract: An extensive area of Norway spruce (Picea abies (L.) Karst.) forests in the Šumava Mountains, Central Europe, has been affected by a massive bark beetle (Ips typographus L.) outbreak since the mid-1990s. One part of the area was left without intervention and two types of intervention have been applied in other parts: (1) the classical forest approach, based on the logging of attacked trees and (2) “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 nonintervention and both types of intervention on the regeneration of the Norway spruce forests. The Norway spruce forests influenced by natural disturbances (bark beetle outbreaks and windfalls) regenerated very well if left without intervention. The bark beetle outbreaks 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 plots, the reduction of both previous vegetation and tree regeneration was obvious. Generally, both interventions against bark beetle delayed the recovery of Norway spruce forests.

Résumé : Dans les monts Šumava, en Europe centrale, une grande étendue de forêt d’épinette de Norvège (Picea abies (L.) Karst.) a été affectée par une épidémie massive du typographe européen de l’épinette (Ips typographus L.) depuis le milieu des années 1990. Une partie de cette superficie n’a subi aucune intervention alors que deux types d’intervention ont été appliqués ailleurs : (1) l’approche forestière classique basée sur la récolte des arbres attaqués et (2) une coupe d’assainissement qui consistait à abattre, à écorcer et à laisser sur place les arbres attaqués. Le principal objectif de notre étude était de tester l’impact de l’absence d’intervention et des deux types d’intervention sur la régénération des forêts d’épinette. Les forêts d’épinette affectées par les perturbations naturelles se sont très bien régénérées en l’absence d’intervention. Le typographe européen de l’épinette et les chablis ne représentent pas une menace pour la pérennité de ces forêts. Les coupes à blanc ont mené à la formation de stades pionniers de végétation suivie d’une régénération d’épinette décalée dans le temps. Dans les peuplements soumis à une coupe d’assainissement, la végétation préétablie et la régénération en épinette ont subi une réduction évidente. De façon générale, les deux types d’intervention visant à contrer les effets du typographe européen de l’épinette ont retardé la remise en production des forêts d’épinette.

[Traduit par la Rédaction]

Introduction

It has been repeatedly demonstrated that long-term persistence of natural coniferous forest ecosystems depends on recurrent disturbances (Bonan and Shugart 1989). Extensive bark beetle outbreaks are one of the most noticeable disturbances of such systems (Schelhaas et al. 2003). Central European spruce forests, both natural and planted, are occasionally subjected to bark beetle (Ips typographus L.) outbreaks, which are similar to the large-scale insect outbreaks that frequently occur in boreal forests (Larsen 1980). Tree species recruitment after a disturbance is a key phenomenon in forest ecosystem development (Pontailler et al. 1997; Ulanova 2000). In Central Europe, there is still a lack of knowledge about the spontaneous development of natural spruce forests after bark beetle outbreaks, because attacked forests are immediately subjected to the traditional forest-management practice of cutting trees (Wermelinger 2004). An extensive forest area affected by large-scale windfalls with subsequent bark beetle outbreaks was left without intervention for the first time in Bayerischer Wald National Park, Germany (Bibelriether 1989). Another similar situation, in which there was a possibility of leaving a forest area without intervention, occurred in the Swiss Alps in the 1990s. Here a large bark beetle outbreak triggered by a windstorm caused the death of almost all spruce trees in an approximately 100 ha area (Lässig 1995).

The effects of artificial disturbance resulting from various forms of intervention against bark beetle outbreaks in forest ecosystems have seldom been studied. Foster and Orwig (2006) found that salvage logging had a negative impact on a forest ecosystem in New England compared with the impact of natural disturbances alone. A similar impact would be expected in 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 (e.g., Dai 1996; Coates...
spruce forests (see below). The tree layer consists almost exclusively of the bog communities and with species typical of such conditions: plants adapted to cold and wet depressions and that occupy the margins of peat bogs characterized by coexistence with species typical of under wet spruce forests (Novaˇk 1993).

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Our study compared natural regeneration of tree species and changes in the cover of the herb-layer in spruce forests after both natural and artificial disturbances, that is, dying trees left after bark beetle outbreaks versus intervention to remove or debark trees. 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 sanitation intervention simulates natural processes.

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Study area

The research was carried out in the central part of the Šumava Mountains (Fig. 1), in natural and seminatural wet 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 a mean annual temperature about 4 °C (Quitt 1971). The bedrock is gneiss that is predominantly created by gneiss partly combined with granites and sandstones. Histosols and gleysols are the prevailing soil types under wet spruce forests (Novák 1993).

The studied forests are wet spruce forests edaphically conditioned to cold and wet depressions and that occupy the margins of peat bogs characterized by coexistence with species of the bog communities and with species typical of spruce forests (see below). The tree layer consists almost solely of spruce, because of the permanently wet soil. Birch (Betula carpathica Willd.) occurs only rarely as an admixture with rowan (Sorbus aucuparia L.) and oak (Quercus robur L.) only as an admixture with spruce (Picea abies (L.) Karst.; hereinafter P. abies) forests in the Šumava Mountains, Czech Republic, part of which were declared a national park, are, in parts, some of the best preserved and least human-influenced spruce forests in Central Europe. Observation of their natural succession after a massive bark beetle attack that occurred in the 1990s provided a unique chance to understand natural processes in spruce forests in general. Unfortunately, large interventions against the bark beetle attack were carried out in the core zone of the Šumava National Park. Besides the classic clear-cutting method, a “sanitation” intervention 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 sanitation intervention simulates natural processes.

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The first important interventions, which significantly influenced and changed the forest structure, started at the beginning of the 19th century (Jelinek 1988). These activities influenced spruce forests, especially on drier sites. Wet spruce forests were influenced rather little, owing to limited accessibility to their wet soils; therefore, they represent the most valuable and preserved spruce stands in the studied region.

Methods

Research plots

A total of 103 transects (10 m × 90 m) were established in selected stands and five 10 m × 10 m sample plots were placed at regular intervals 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 outbreaks, and with or without intervention against bark beetle. According to these criteria, plots were divided into four groups: Plots without intervention, (1) green canopy, that is, undisturbed or very slightly disturbed unmanaged stands composed mainly of live trees, tree can-

opportunity cover >25% (115 plots) and (2) dead canopy, that is, dead or partly dead stands with tree canopy reduced by natural disturbances such as bark beetle attack and partly uncleared windthrows, tree canopy cover <25% (155 plots), in which trees died gradually from 1997 to 2001 and plots with intervention against bark beetle, (3) clearcuts, that is, stands without canopy (attacked by bark beetle and completely cut down), 0%–25% of cut debarked trees left lying on the site (159 plots) and (4) sanitation plots, that is, stands without canopy, in which trees attacked by bark beetle were cut down, debarked, and all left on the site (86 plots). Cutting and sanitation interventions were performed between 1997 and 2001. Information on management was provided by the national park administration.

Data collecting

All data were collected in 2002. Tree canopy cover was evaluated visually in the 10 m × 10 m plots. A 3 m × 3 m plot was marked in the center of each plot, where natural regeneration was measured by recording the numbers of seedlings of all tree species. Seedlings were divided into the following height categories: (i) spruce 1, <10 cm; 2, 10–20 cm; 3, 20–100 cm; and 4, 100–300 cm; (ii) broad-leaved species 1, <20 cm; 2, 20–50 cm; 3, 50–100 cm; and 4, 100–300 cm.

Microhabitat types covering the forest floor were defined and their extents in each 3 m × 3 m plot were recorded. The microhabitats analyzed included lying logs (nondebarked) in all states of decay, debarked logs (resulting from sanitation interventions), patches of herb layer in total, Sphagnum sp. patches, patches of other mosses in total, root plates (roots of uprooted trees), and slash (the remnants of branches originating mostly from cutting and logging interventions). The extent of each microhabitat was determined by visually estimating its percent cover in each plot.

Vegetation was evaluated by visually estimating percent cover of all herb species and the moss layer (divided into Sphagnum sp. and other mosses) in the central 3 m × 3 m plots. The nomenclature of vascular plants and mosses was done according to Kubát et al. (2002) and Kučera and Váňa (2003), respectively.

Statistics

The variability in number of seedlings for the tree species split into height categories in relation to explanatory variables was first analyzed by redundancy analysis (RDA) using Canoco® (Ter Braak and Šmilauer 1998). Management (disturbance type and canopy cover) and microhabitat (extent 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 possible different effect of time in the two types of intervention on seedling numbers was tested using interaction between intervention type and time; the numbers of seedlings of each tree species was square-root transformed in all analyses. The statistical significance of the relation with explanatory variables was tested by the Monte Carlo permutation test. The resulting ordination diagrams were produced using CanoDraw® (Ter Braak and Šmilauer 1998). Vegetation pattern in relation to management regime was also evaluated by RDA. Covers of herb-layer species were used as response data and management regime types were used as explanatory variables. The influence of time from intervention was evaluated only for data from intervention plots as it was for natural regeneration. Differences in total numbers of spruce and rowan seedlings, extent of microhabitat types, mean number of species per plot, and mean number of forest species per plot among disturbance types were tested by one-way ANOVA (Statistica® version 6.0). In the case of significant effects (p < 0.05), post-hoc comparisons were made using Tukey’s honestly significant difference (HSD) test.

Results

Multivariate analysis of natural regeneration of tree species

Seedlings of five tree species were found. RDA showed the significant influence of management (disturbance type and canopy cover), microhabitat, and time elapsed from human intervention (Table 1). The effect of time did not differ between clearcuts and sanitation plots (nonsignificant interaction between time and disturbance type). The number of
seedlings of all species related to the compared types of stands and canopy cover are shown in Fig. 2. The greatest difference appeared to be 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 (willow (Salix sp. div.), birch (Betula sp. div.), and aspen (Populus tremula L.)) were strictly correlated with plots managed against bark beetle. Spruce and rowan seedlings were prevalent under canopy. Rowan and taller spruce seedlings were predominantly found under dead canopy (<25% cover), while spruce seedlings of lower height categories were prevalent under green canopy (>25% cover).

The relationships between various microhabitat types and number of seedlings of each tree species are shown by the RDA results in Fig. 3. The first ordination axis separated all broad-leaved species except for rowan seedlings in the lowest height category from spruce seedlings in all height categories. Spruce seedlings were correlated with nondebarked logs, root plates, and mosses, including Sphagnum sp. and lower herb-layer cover. Broad-leaved species predominated in plots with brushwood, debarked logs, or a higher herb-layer cover. Microhabitat explained the greatest part of the variability in the species data (28.5%).

Time elapsed from intervention seemed to be the least important factor, explaining only 1.9% of variability in the data from the intervention plots. The effect of time did not differ between clearcuts and sanitation plots (nonsignificant interaction). Time had a slight positive influence on the number of seedlings in higher height categories, especially rowan, willow, and birch.

**Number of tree seedlings**

Spruce seedlings formed the greatest part of the regeneration. The numbers per hectare were several times higher under canopy than in clearcuts and sanitation plots, and varied significantly among disturbance types (ANOVA, $F = 11.3$, $p < 10^{-6}$). The mean number of seedlings was about 30,000 seedlings/ha under dead canopy and almost 50,000 seedlings/ha under green canopy. About 10,000 seedlings/ha were found in sanitation plots and only a few thousand in clearcuts (Fig. 4). The highest numbers of birch, willow, and aspen seedlings were found in clearcuts, and no seedlings occurred under green canopy. Rowan seedlings occurred established themselves differently than other broad-leaved trees did. The highest numbers of seedlings were found under dead canopy (>700 seedlings/ha; ANOVA, $F = 6.28$, $p = 0.0003$), while similar numbers were found in all other types of plots: about 200 seedlings/ha in plots without canopy and 300 seedlings/ha under green canopy.

**Microhabitat occurrence**

The cover of particular microhabitat types varied significantly among disturbance types (ANOVA, $p < 10^{-6}$; Fig. 5). Total herb-layer cover was greatest in clearcuts and under dead canopy. Mosses including Sphagnum sp. were prevalent under green canopy, but also survived quite well under dead
canopy compared with clearcuts and sanitation plots. Nonde-barked logs and root plates occurred predominantly under dead canopy. Sanitation plots featured the least herb layer and moss covers.

Vegetation composition
Species composition of the herb layer was significantly influenced by management and, in the intervention plots, by the time elapsed from intervention (Table 1). Vegetation composition seems to be influenced less by environmental factors than natural regeneration of tree species (environmental factors explained a smaller part of the 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). Species typical of spruce forests were almost absent in sanitation plots; the species found there were typical of clearcuts.

The time elapsed from intervention positively influenced the increase of the herb-layer cover (Fig. 7). The cover of only a few forest species decreased over time. Also, the cover of some pioneer species that occurred immediately...
after intervention decreased. The effect of time on vegetation composition did not differ between clearcuts and sanitation plots (Table 1).

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

Discussion

The influence of disturbance type on natural regeneration

The type of disturbance significantly influenced the natural-regeneration structure in the studied wet spruce forests. Time elapsed from intervention had only a minor effect, so all plots can be compared despite their slightly different ages. Spruce formed the greatest part of regeneration in all types of plots, but were more frequent in plots with green canopy. This result is different from those obtained in previously managed spruce forests, in which more spruce seedlings were found under dead canopy than under green canopy (Nühlein and Faßt 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; Drobyshiev 1999). Nevertheless, the studied wet spruce forests had a relatively open canopy (about 40% cover) before the disturbance, which may be the reason that canopy reduction after bark beetle attack did not have the same positive effect on spruce regeneration as in the managed spruce forests with a relatively closed canopy. Moreover, there are more microhabitats suitable for spruce regeneration in wet spruce forests than in managed forests. The numbers of seedlings, especially in low age categories, are often higher than in spruce forests on drier sites, probably for the same reason.

The low numbers of seedlings in clearcuts were probably caused by spruce sensitivity to removal cutting, which usually results in a high mortality rate in spruce seedlings (Nilsson et al. 2002). Leaving debarked logs in plots seems to be a better option for spruce regeneration than clear-cutting. Nevertheless, both types of intervention against bark beetle caused a great reduction of spruce regeneration compared with that in dead stands. Forestry interventions against bark beetle largely reduce the youngest generations of seedlings in spruce forests (Jonášová and Prach 2004).

Rowan seedlings were the most numerous of the broad-leaved species and, as the only species, had the most seedlings under dead canopy. In contrast to the other observed species, rowan can be easily spread over large distances by birds (Leder 1997). Clearcuts and sanitation plots are not very attractive for birds, and this limited the spread of rowan in the study site. Vanha-Majamaa et al. (1996) also recorded the highest rate of regeneration of rowan particularly in the shade of dead trees. Open canopy is necessary for its growth and flowering, although seedlings and small saplings are tolerant of shade (Grime et al. 1988). Increasing rowan numbers seems to be a typical phenomenon in stands left without intervention after bark beetle attack and its importance for natural regeneration in damaged spruce stands was reported by Weihs (1995) and Leder (1996).

Other broad-leaved species (birch, willow, and aspen) clearly predominated in clearcuts, with only a minor number of seedlings being found under dead canopy and in sanitation plots. These species have high light requirements and are considered pioneers in succession (Grime et al. 1988). Lässig (1995) found an increasing number of pioneer broad-leaved species with increasing size of clearings. In our case, light conditions in the clearcuts and sanitation plots were the same, because they were similarly large and the tree layer was completely removed in both of them. The lower number of pioneer broad-leaved species in sanitation plots can probably be attributed to a lack of favorable microhabitats such as a disturbed soil surface.

The influence of microhabitat structure on natural regeneration

Favorable microhabitat structure appeared to be a key factor for successful regeneration of wet spruce forests. This is supported by the results of RDA, in which microhabitat explained more of the variability in the species data than disturbance type. Consequently, it is likely that the nature of regeneration was influenced more by suitable microhabitat structure than by canopy closure. The occurrence of spruce seedlings was correlated with nondebarked 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 (Hofgaard 1993; Szewczyk and Szwarzgryk 1996; Hörnberg et al. 1997; Kupferschmid and Bugmann 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 broad-leaved species were not so clear; nevertheless, branches and parts of dead trees are important for all broad-leaved species as protection against browsing, which is a common problem in this region (Matějková and Jonášová 2002).

The most severe change in microhabitats occurred with wood removal, resulting in the loss of potential microhabitats for spruce seedling establishment. Dead wood, in addition to large living trees and snags, is one of the most important

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<th>Table 2.</th>
<th>Total and mean numbers of herb species in different disturbance types.</th>
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<td>Disturbance type</td>
<td>Green canopy</td>
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<tr>
<td>Total no. of species</td>
<td>30</td>
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<tr>
<td>Percentage of forest species in total number of species</td>
<td>46.7</td>
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<td>Mean no. of species per plot (3 m x 3 m)</td>
<td>4.1a</td>
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Note: Post-hoc comparisons of mean numbers were tested by Tukey’s HSD test. Values followed by different letters are significantly different.
components of natural spruce forests and, at the same time, important for spruce regeneration (Siitonen et al. 2000). Its importance is now acknowledged even in production forests (Meyer 1999). In this respect, bark beetles act as a positive factor in the development of a more natural forest structure.

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

Vegetation composition

Relative light level, controlled by canopy dynamics, is a key factor determining the dynamics of the herb layer (Nabuurs 1996). The total number of species and the number of species per plot were highest in clearcuts, which corresponds to other results (e.g., Fischer et al. 1990; Pykälä 2004). However, the share of higher plant species typical of spruce forests was lowest in clearcuts. These results indicate that total species number cannot be used as an indicator of the condition of a community, because artificial disturbance led to an increased number of weedy species at the expense of late-successional species. Among all plants, mosses were the most sensitive to disturbance (Jalonen and Vanha-Majamaa 2001). Their rapid decrease in clearcuts and sanitation plots compared with dead stands showed the relatively low influence of bark beetles on moss abundance compared with that in artificial disturbances.

Conclusions

The natural regeneration of trees and changes in the herb and moss layers after artificial disturbance differed distinctly from regeneration after natural disturbance. Natural disturbance encouraged natural regeneration of the original species of spruce forests without leading to extensive changes in vegetation structure. On the contrary, both types of interventions against bark beetle observed substantially damaged the original forest vegetation and natural regeneration. Although sanitation is supported by forest management as being close to nature, the results are very different than natural disturbance results and similar to those after clear-cutting. The sanitation plots are not favorable for regeneration of either the original species, as in dead canopy, or wind-dispersed pioneer species, as in clearcuts. Nevertheless, sanitation still appears to be a better choice than clear-cutting for maintaining the forest community: spruce seedlings survived here more successfully than in clearcuts and pioneer vegetation did not expand. In contrast to both types of intervention, disturbance caused by bark beetle attack had a positive effect on original-species regeneration and helped the natural forest structure to recover. The nonintervention strategy should be used as much as possible in protected areas rather than any technical forestry interventions.

Acknowledgments

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