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Progress of forest regeneration after a large-scale *Ips typographus* outbreak in the subalpine *Picea abies* forests of the Bavarian Forest National Park

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Abstract
The Bavarian Forest National Park is the oldest National Park in Germany. The overall management concept within the park is the protection of unaltered natural processes. The outbreak of a spruce bark beetle (*Ips typographus*) infestation in 1993 has especially affected the subalpine range of the park with its high proportion of spruce trees. This paper describes a study on how forest regeneration was affected by the process of the large-scale die off of forest trees. For this purpose, surveys from a total of 572 samples from the years 1991, 1996, 1998, 2000, and 2005 were available. Compared to 1991, when the regeneration density was 978 trees per hectare, it had increased to 4502 trees per hectare in 2005. The distribution of the regeneration has also changed. While in 1998, only 36.7% or the inventory plots were found to have a density of greater than 1000 plants per hectare, this value had increased to 62.4% by 2005. No regeneration was found in only 0.9% of the inventory plots. Regeneration consisted mostly of Norway spruce (89.0%) and mountain ash (7.9%). European beech (1.9%) and all other tree species (1.2%) were much less significant. In addition, the proportion of tree heights has clearly shifted to taller trees. This indicates a favourable development of the trees in the regeneration. The proportion of trees damaged by browsing ungulates was 1.6%. Browsing damage to mountain ash was relatively high at 33.6%. Other forms of damage were relatively insignificant.

Key words: forest regeneration, subalpine spruce forest, bark beetle, disturbance, Bohemian Forest

Introduction

The year 1993 was the beginning of a development that have dramatically alterred the subalpine Norway spruce forests of the Bavarian Forest National Park. The spread of the Norway spruce bark beetle (*Ips typographus*) began in small, scattered patches that were soon distributed throughout much of the subalpine forest. In 1995 the beetle population virtually exploded. Within one year, 310 ha of the subalpine Norway spruce stands had died off. The development of the beetle population reached a peak the following year when 583 ha of matured forest were "consumed". Afterward, the rate of infestation in the subalpine ranges decreased because most of the mature Norway spruce had already died-off. Meanwhile, 2031 ha of the subalpine range had been affected by spruce bark beetle (Heurich 2001, Heurich & Rall 2006).

In managed forest stands elsewhere, mass reproduction of the Norway spruce bark beetle has always been combated, and the resulting clear-cut areas have been reforested immediately. After the die-back of the old stands in the National Park, it was questioned whether regeneration of the forest would be able proceed at all. Such uncertainties were based especially on the extremely rapid rate and large extent of the area in which the trees had been killed, as well as the unfavourable conditions prevalent at the high elevations. Considering the often tempered discussions, that have been going on among forestry experts for well over a century, on how to best manage the subalpine forests, this question seems justified. Just as it does today, the discussion has always revolved around the question of how it would be possible to guarantee sufficient regeneration of the forest stands. And just as they were then, opinions on the mater are divided as to whether any measures – and if so, what kind – are necessary to preserve the forest.

From a research perspective, this event is a highly rewarding object for investigation. Although there have been numerous studies on the regeneration of near-natural ecosystems after disturbances, they have either been from North America, concerned other tree species, or occurred in relatively small reserves (Rykiel 1988, Romme & Despaine 1989, Lässig et al. 1995, Wermelinger et al. 1995, Perry 1997, Turner et al. 1997, Kupferschmid 2003, Jonášová & Prach 2004). In Central Europe, it has not been possible to gather experience with processes as they have developed after large-scale die-offs of mature trees or with the effects on the natural communities in areas not influenced by human intervention.

Therefore, the emphasis of this paper is to document the progress of forest regeneration in the entire subalpine range within the core zone of the National Park. For this purpose, 572 sample plots, evenly distributed throughout the entire subalpine zone, were studied between 1991 and 2005. The goal was to monitor the temporal and spatial progress of changes in the density of regeneration, the tree species composition, relative heights, and damages to individual plants.

Material and methods

Study area

The high altitude, or subalpine, range of the Rachel–Lusen region of the Bavarian Forest National Park is situated between 1050 m and 1453 m a.s.l. Temperature is a determining factor for plant growth. The average annual temperature is only 3.0–4.5°C (Elling et al. 1987). The high precipitation level (1300–1800 mm) and its distribution, with a primary maximum in summer and a second maximum in winter, provide a favourable water supply during the short growing season; 50% of the precipitation falls as snow. Combined with the low temperatures, this results in snow cover for an average duration of seven months, from October to May.

The main soil types are brown dytrophic cambisols with a more or less prominent tendency to podzolisation. These soils were formed from weathered material originating in the underlying granite and gneiss layers. The low alkaline content of the original substrate results in acidic to highly acidic soils with pH values of 2.4 to 2.8 (in KCl) in the organic layers and 4.5 in the deeper horizons. These soils are characteristic with a layer of solidified debris at a depth of 30–60 cm. Even with tools, it is difficult to break up and work this layer. It limits the depth, to which tree roots are able to penetrate, and reduces the permeability of the soil. Especially the growth of European beech (*Fagus sylvatica*) is inhibited under these conditions. On this solidified debris, the trees are only capable of stunted growth. The most common soil type in the high altitude range is loam of intermediate depth over the underlying solidified debris; 12% of this area is covered with mineral and organic wet soils. They are primarily a result of the high precipitation. The ledge and talus surfaces are also significant (with 12%). They are concentrated in the steeper locations and are characterised by large-scale ledge formations and coarse skeletal soils. In these locations, root penetration is limited to the mineral fill between blocks of stone and to an overlying, more or less thick layer of raw humus. Under such unfavourable climatic and edaphic conditions, mineralisation of the litter above and below the ground level remains incomplete. This results in a 2–19 cm (average 8 cm) thick horizon typically composed of raw humus and raw humus-like moder (Elling et al. 1987).

The spatial delineation of the subalpine range was defined by Elling et al. (1987) according to the morphology of the landscape and edaphic criteria. The high altitude range begins where the relatively steep slopes angle off or transform into the rounded, rolling hills that make up the ridge of the Bohemian Forest. The duration of the snow cover above these slopes is much longer than in the areas below. It also corresponds to the level above which the montane mixed forest of the slopes is succeeded by the montane spruce forest. The precise delineation of the high altitude range was determined by a characteristic of the soil: it is above the upper limit of the loose brown soils (Lockerbraunerde).

Data collection

The foundation of the forest regeneration survey is a network of sample plots that were laid out for forest inventories in 1991. These permanent reference plots are arranged in a 200×200 m grid over the entire area of the National Park. The inventory plots were marked in the field with iron pipe survey markers, magnets, and plastic ribbons in order to facilitate finding their location in subsequent surveys. This guarantees that the same survey plots will be used for each inventory and ensures reproducibility of the results.

Of the total 6000 inventory plots in the entire National Park, only 572, which are located in the 2300 ha subalpine range of the Rachel–Lusen area, were used for the evaluation. The fieldwork was carried out from June to August in the years 1991, 1996, 1998, 2000, 2002, and 2005.

In order to guarantee comparability of the results, the survey concept of the past years was adhered to. Therefore, it is now possible to describe the dynamics of forest regeneration since 1991 when the first survey was performed. As before, measurements were taken in concentric circles, within which young trees between 10 cm and 5 m in height were inventoried according to graduated calliper thresholds. The size of the area within which trees of 0–5.9 cm diameter at breast height were inventoried was 25 m²; for trees of 6 to 11.9 cm DBH (diameter at breast height) the area was 50 m². Species, height, and damages (browsing, snow breakage, etc.) were recorded for each tree. The following height classes (in cm) were distinguished: 10–20, 20–39, 40–59, 60–79, 80–99, 100–149, 150–199, 200–299, 300–500.

In order to guarantee the high quality of the data, 10% of the sample plots (= 57 plots) were subjected to a second control survey. Analysis of the first and control surveys assured a high degree of accuracy. The design of the sampling system corresponds to the standard methodology used by the Bavarian Forest Administration (Bayerisches Staatsministerium für Landwirtschaft und Forsten 1982) (Fig. 1).

Since the permanent sample plot inventory, as based on the above-mentioned methodology, was conceived as a forest management inventory, it only allows a limited interpretation of the spatial distribution of the forest's regeneration. In spite of this, more information on the spatial distribution of the regeneration process was sought by modifying the existing inventory system and increasing the area of the circular sample plots to 500 m². Using this modified method, an area with a diameter of approximately 25 m was investigated. In the subalpine range, this corresponds roughly to the height of a mature tree. In order to limit, to a reasonable degree, the additional expenditure caused by increasing the size of the sample area, young trees between 20 cm and 5 m in height were counted only up to a threshold of 50 plants. In a flat landscape, this would correspond to 1000 plants per hectare. Species, height, and damages were not recorded for these trees. If less than 10 plants could be found

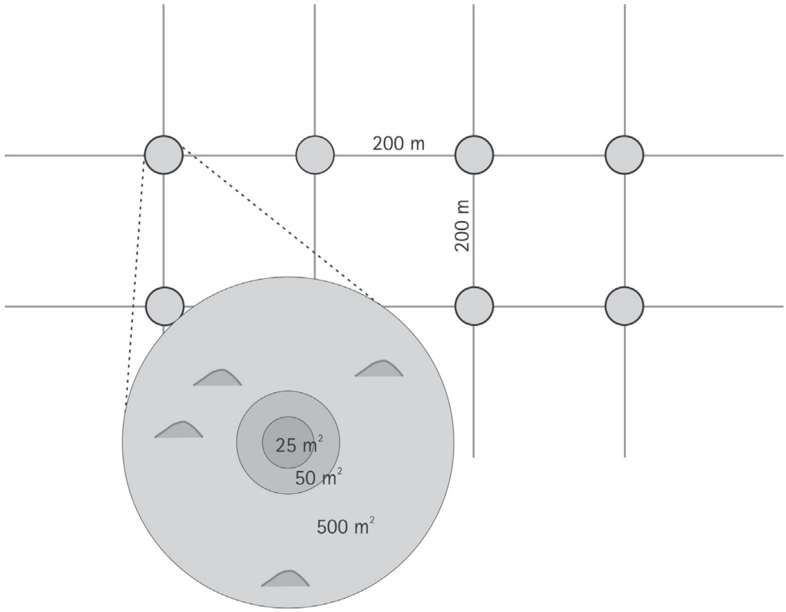

Fig. 1. Sampling design for the high altitude inventory.

that were taller than 20 cm, an additional 10 plants with heights between 10 and 20 cm were counted as well (Grünvogel & Heurich 2002). Since practically the same survey was carried out in 1998, the results from that inventory (Nüsslein 1998) can be compared directly with those from the recent survey. Slight deviations in frequency distribution compared to those published by Nüsslein (1998) are due to the different number of inventoried sample plots. While in 1998, additional sample plots between the permanent inventory plots were recorded (a total of 1639 circular sample plots), the recent inventory included only 572 permanent inventory plots. The comparison between the frequency distributions is based only on the 572 plots that were surveyed in1998, 2002, and 2005.

Results

Development of regeneration density

Analysis of the surveys in the 25 and 50 m² circular sample plots of the permanent sample plot inventory in the subalpine range of the Rachel–Lusen area yielded a mean regeneration density of 4502 plants larger than 20 cm per hectare. This means that the regeneration density had increased by nearly 70% since the last inventory in 2002. The positive trend in the development of regeneration that has been observed since 1996 continues. Compared to the reference year 1991 – before the mass reproduction of the Norway spruce bark beetle, and when the regeneration density was 978 plants per hectare – the number of young plants has more than quadrupled (Fig. 2).

The increase in regeneration density since the last inventory in 2002 is due almost exclusively to one species: Norway spruce. The regeneration density for this species increased by 76% to 4033 plants per hectare. For mountain ash, the regeneration density increased only

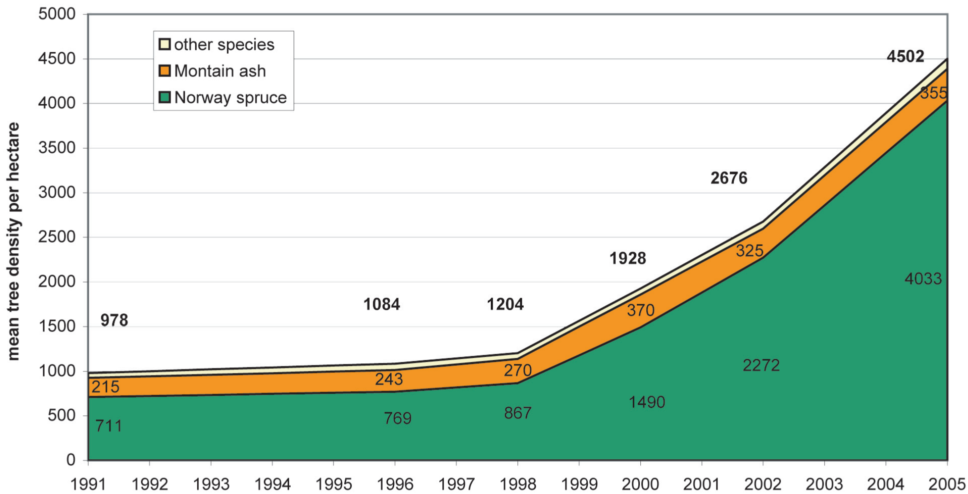

Fig. 2. Development of regeneration density for the trees taller than 20 cm.

insignificantly from 325 to 354 plants per hectare. For all other tree species, the regeneration density increased by 45% to a current value of 114 plants per hectare.

In addition to the plants taller than 20 cm, which, at that size, can be considered established, plants between 10 and 20 cm in height were also counted. These small plants are much more susceptible to numerous dangers, and for this reason, they are treated separately here. These plants are of great importance for the further development of the forest, however, since in the course of the next several years, some of them will have passed the 20 cm threshold. In 2005 the average number of plants in this category per hectare was 738 (Table 1).

Compared to the value of 1895 plants in this category per hectare, which was determined in 2002, this is a decrease by more than half. However, the value observed in 2005 is still higher than the values from 1996 and 1998. For comparison, the number of plants per hectare in this height category was only 630 in 1998 and 614 in 1996. The great majority of these plants were Norway spruce (687); the additional mixed tree species comprised only 14

Table 1. Development of the regeneration density of plants taller than 20 cm in height since 1991 by tree species.

	1991		**1996**		**1998**		**2000**		**2002**		**2005**	
	N/ha	**%**	**N/ha**	**%**	**N/ha**	**%**	**N/ha**	**%**	**N/ha**	**%**	**N/ha**	**%**
Norway spruce	711	72.7	769	70.9	867	72.0	1490	77.3	2272	84.9	4033	89.6
Mountain pine	7	0.7	1	0.1	1	0.1	1	0.1	0	0.0	1	0.0
European beech	32	3.3	46	4.2	61	5.1	55	2.9	61	2.3	86	1.9
Sycamore maple	0	0.0	4	0.4	1	0.1	2	0.1	1	0.0	2	0.0
Silver birch	0	0.0	1	0.1	2	0.2	3	0.2	6	0.2	19	0.4
Mountain ash	215	22.0	243	22.4	270	22.4	370	19.2	325	12.1	355	7.9
Willows spec.	14	1.4	20	1.8	2	0.2	7	0.4	0	0.0	5	0.1
Aspen	0	0.0	0	0.0	0	0.0	0	0.0	11	0.4	1	0.0
Total	**978**	**100.0**	**1084**	**100.0**	**1204**	**100.0**	**1928**	**100.0**	**2676**	**100.0**	**4502**	**100.0**

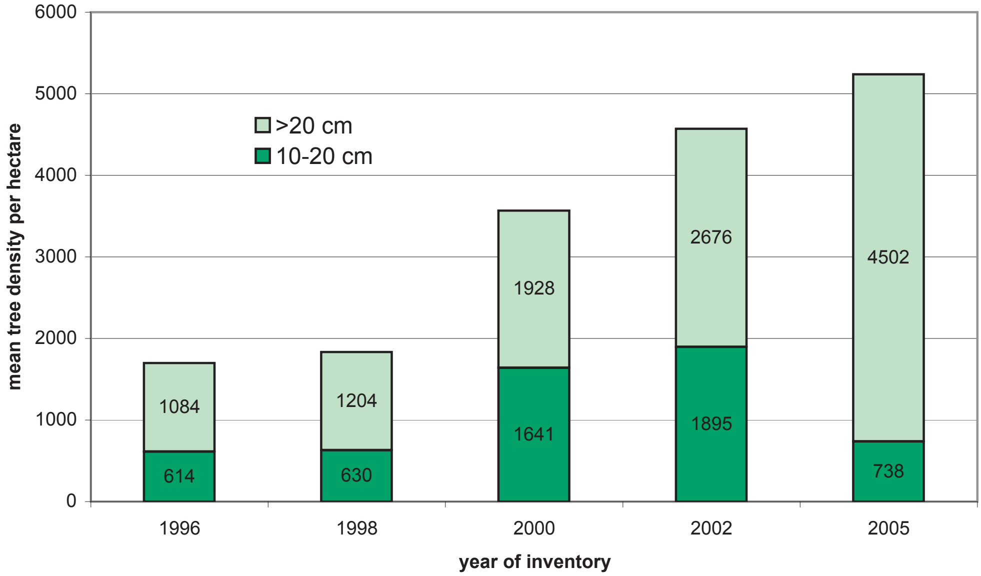

Fig. 3. Development of the regeneration density of trees taller than 10 cm in height since 1996.

Mountain ash and 37 European beech. If all plants taller than 10 cm are taken into account, the mean regeneration density increases to 5240 plants per hectare. This is an increase of 15% over the value from 2002 (Fig. 3).

Development of the relative proportions of trees species

In 1991, before the beginning of the mass reproduction of the Norway spruce bark beetle, Norway spruce was the dominant tree species in the subalpine forests. Then, it comprised 98% of the total timber volume. The remaining 2% were made up of European beech (1.2%), mountain ash (0.4%), sycamore maple (0.2%), and other tree species (0.2%) (Rall 1995). The tree species composition of the regeneration layer between 20 cm and 5 m differed significantly from that of the mature stands. There, the proportion of Norway spruce was only 73%. The second most common tree species was the mountain ash with 22%, and the third most common was the European beech with 3%. All other tree species together comprised only 2% (Heurich 2001).

The trend that has been observed since 1996, with an increasing proportion of Norway spruce, has continued unbroken till 2005. While its proportion in the year 2000 was still 77.3%, in the meantime it had increased to 89.6%. In contrast, the proportion of mountain ash decreased to 7.9%. The proportion of other tree species also decreased to ca. 2.5%. The species with the largest percentage in this group was the European beech with 1.9% (Fig. 4).

This trend is even more conspicuous if only plants between 10 and 20 cm are considered. In this case, the proportion of Norway spruce increased from 84 to almost 97% in the period between 1996 and 2002. Since the last inventory, the proportion of Norway spruce in this height category has decreased to ca. 93%.

Considering all plants taller than 10 cm together, the proportion of Norway spruce is 90.1%, the proportion of mountain ash is 7.0%, and the proportion of all other tree species is only 2.9%.

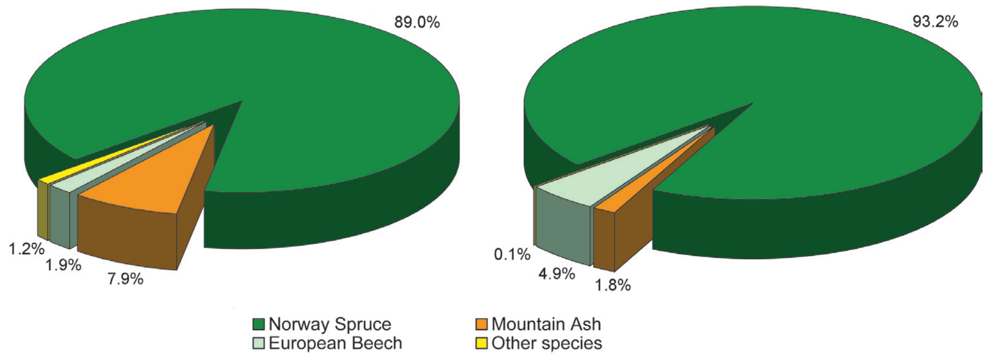

Fig. 4. Proportions of tree species >20cm (left) and proportions of tree species >10cm (right).

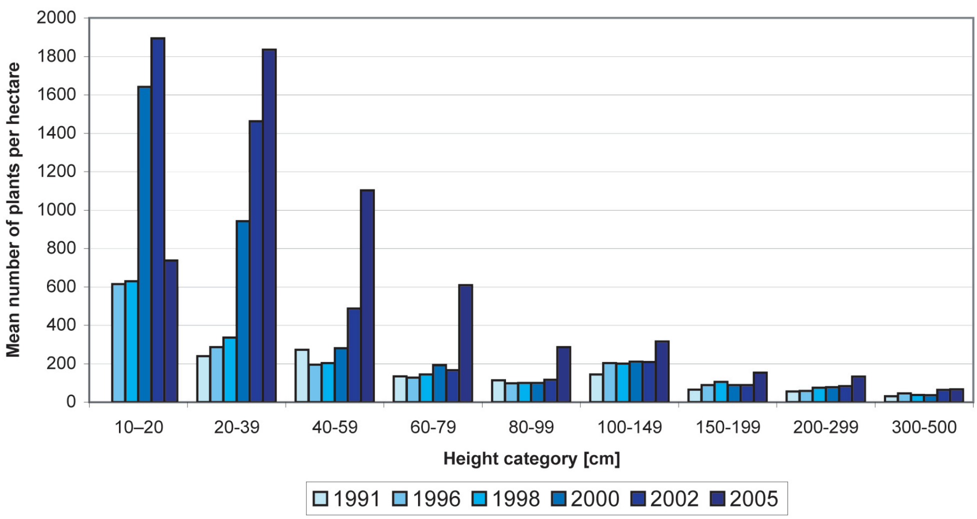

Fig. 5. Development of the height composition in the forest regeneration.

Development of height composition

To better illustrate the development of height composition, nine height categories were established. Since the last inventory, the numbers of trees in all height categories have increased. The only exception is for the trees between 10 and 20 cm in height (Fig. 5).

While in the period between 1991 and 2002, only trees in the height categories > 60 cm increased in number, the 2005 inventory revealed an increase in the number of trees per hectare for all height categories between 20 and 300 cm.

Development in relation to damages to individual plants

During the survey, the presence of browsing damage to the leading shoots of the regeneration since the last growing season was documented. The only significant browsing damage was caused by ungulates (roe and red deer). While browsing damage to Norway spruce has continuously decreased, reaching a value of only 1.6% by 2005, the amount of browsing damage to the lead shoots of mountain ash was found to have increased since 2000. In 2005

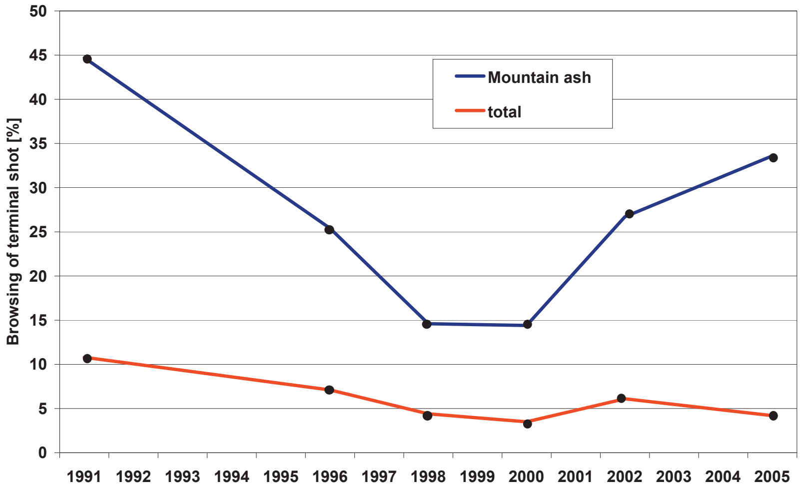

Fig. 6. Development of browsing damage caused by hoofed game to terminal shoots.

the damage level was at 33.6% (Fig. 6).

A total of 49 plants showed signs of snow breakage. Beyond this, no other notable damage to the regeneration plants was observed during the surveys.

Spatial distribution of the regeneration

The comparison of the distribution of regeneration densities in the 25 m² and 500 m² plots show that regeneration is clustered on a scale beyond 500 m². Young trees measuring more than 20 cm in height were found in 99.1% of all the circular plots. Assuming that the plots, which are evenly distributed throughout the subalpine range, are representative for the entire area, this would mean that there is at least some regeneration in practically all parts of the subalpine range. Only five plots were found to lack regeneration completely. If plants between 10 and 20 cm in height are taken into consideration, the number of plots without regeneration is reduced to two. In mature stands, in which mature trees are usually present, regeneration was almost always found. This means that the situation has improved markedly when compared to 1998: at that time, 6.3% of the plots were without regeneration. There is also a general trend indicating a shift in the frequency distribution towards greater regeneration densities. While the number of circular plots with less than 500 plants per hectare decreased from 32.7 to 20.8% since the previous inventory, the number of plots with more than 500 plants per hectare increased from 62,8 to 79.2%. The percentage of plots with more than 1000 plants per hectare increased from 41.6 to 62.4% (Figs 7–9).

The pattern of distribution of the regeneration density for the sample plots over the entire subalpine range has changed. Formerly, there appeared to be obvious differences between certain major areas. On the one side, there were the eastern part of the subalpine range – between “Böhmweg” and “Siebensteinkopf” – and the lower areas of the transition zone to the montane mixed forests on the slopes. On the other side, there were the areas west of the “Plattenhausenriegel” and near the peak of the Rachel massif. Now, these differences are becoming more balanced. Although the area of the Rachel massif still has the least regeneration, the situation in the majority of the sample plots has improved since the previous inventory. The development in the area between Rachel and Lusen was even better.

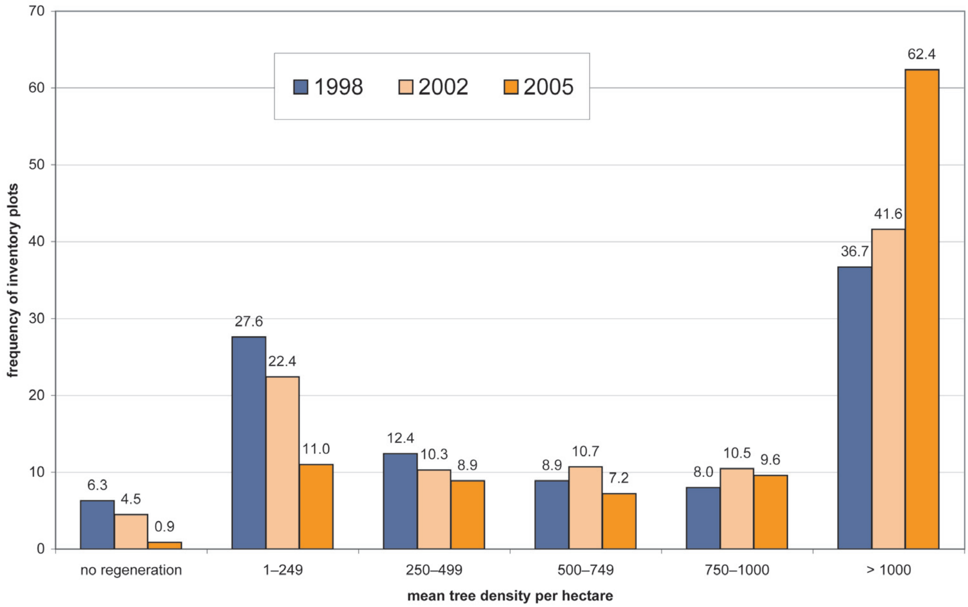

Fig. 7. Frequency distribution of the regeneration density in the 500 m² sample plots.

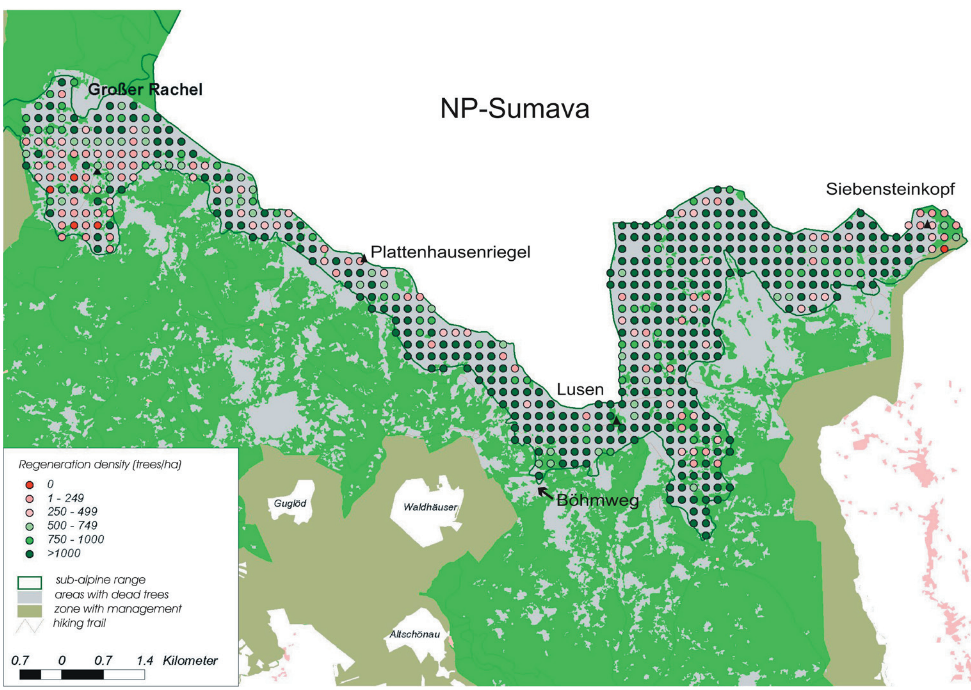

Fig. 8. Regeneration density in the sub-alpine range of the Rachel–Lusen area in 2005.

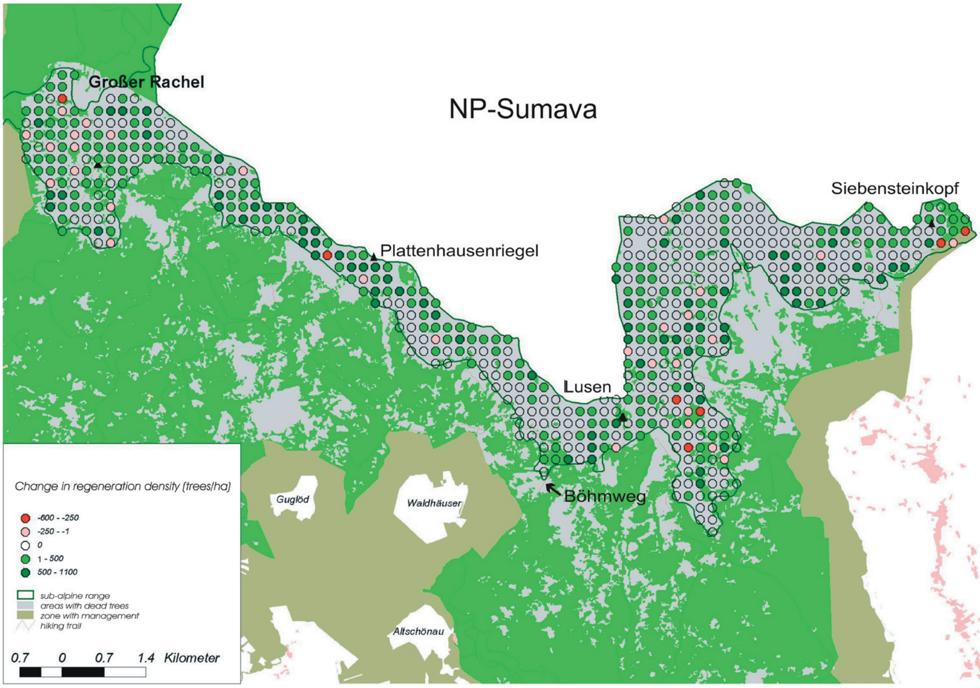

Fig. 9. Change in regeneration density in the sub-alpine range of the Rachel–Lusen area between 2002 and 2005.

Discussion

Regeneration density

Due to the loss of the upper tree layer, the young plants that had already been present before the die-off in 1991 initially showed a positive reaction. In spite of this, however, the regeneration densities determined in the 1996 and 1998 inventories were relatively low. Since the 2000 inventory, a strong increase in the regeneration density was recorded. This especially involved the smaller plants. The reason for this development goes back several years: it was the intense Norway spruce blossom and successful cone production of the 1995 season that resulted in a carpet of Norway spruce seedlings in selected favourable locations in the early summer of the following year. Nonetheless, these miniature trees were exposed to numerous hazards. Since the small roots are not able to penetrate through the humus and into the mineral layer of the soil, even a short drought would kill off thousands of seedlings. March mushrooms (*Hygrophorus marzuolus*) and snow-creep can also kill numerous plants. 84% of the 360 000 seedlings per hectare, that Ott et al. (1997) counted in a Norway spruce forest near Davos, Switzerland in 1982, had died by the end of 1984. When the surveys were repeated nine years later, none of the seedlings were left. Plants resulting from the mast year of 1958 in the Bavarian Forest met a similar fate: in spite of extensive soil treatment and fertilisation, only very few survived. Bauer (2002) documented a significant reduction in the number of young plants that was not as drastic as in the above-mentioned Swiss study: 21 400 of 29 400 seedlings counted in 1998 were still present in 1999.

The fact that, this time, more seedlings survived than in the Swiss example and in the past study might have to do with an alteration in the microclimatic conditions caused by the bark beetle infestation. Analysis of the sample plots, sorted according to the year of the die-off, that numerous young plants became established especially in areas, in which the old stands had died off in 1996. Even though many seedlings in these areas were covered with falling needles and eventually died, the improved light and temperature conditions promoted the survival of a greater than average number of seedlings. In contrast, in the areas, in which the mature trees died off one year later, the average regeneration density was only half as high. Therefore, it may be concluded that the mast year of 1995 was responsible for a huge increase in the number of plants. This is in accordance with findings by Ammer (1998) who observed that young spruce seedlings are able to survive in shade, but they need more light to start growing; moreover, seedlings need more light to grow well under unfavourable site conditions.

Compared to Norway spruce, the development of mountain ash has been much more consistent. This is because of the more or less continuous seed production in this tree species, which due to the small number of mature trees, proceeds at a low rate and is not restricted to a few mast years, which can often be years apart. In spite of an increase in the absolute number of mountain ash, the relative proportion has decreased steadily. This is because of the much greater increase in the absolute number of Norway spruce. These results support the observations of Jehl (1995) and Hildebrand & Rosenberg (1996), who saw the mountain ash less as a pioneer species, but rather as a species of semi-shaded areas that became more easily established under the loose canopy than in open areas.

Other pioneer tree species occur in only small numbers in the subalpine range of the Bavarian Forest. Their role in the regeneration of the forest has been insignificant. This is partly due to the fact that pioneer tree species rejuvenate mostly in areas with exposed mineral soils (Lässig & Schönenberger 1993, Homann & Engels 1991). Such small-scale structures are not as prevalent after a Norway spruce bark beetle infestation as they would be in a situation after windthrow or in clear cut areas (Jonášová & Prach 2004).

The proportion of European beech has changed only insignificantly in the past years. There has been much discussion about the effects of the prognosticated climate change and that, as a result, European beech might be able to extend its distribution range into the subalpine forests. However, since European beech is not adapted to the climatic conditions of the open areas, this will be a very long process (Kupferschmid et al. 2002, Schönenberger 2002). For this reason, the regeneration of European beech is currently concentrated mostly in the vicinity of montane mixed forests, in which surviving mature European beech trees are able to attenuate the climatic extremes. The expansion of grasses into the open areas, which are usually accompanied by increased densities of mice, is also disadvantageous for an increase in the proportion of European beech (Hohenadel 1981). It is likely that many beechnuts are consumed and that the bark of the saplings is gnawed away, both resulting in high losses. As a shade species that requires a more balanced inner-forest climate, European beech will not be able to penetrate the montane Norway spruce forest until after an initial forest of mountain ash and/or sparse stands of Norway spruce have become established (Hildebrand & Rosenberg 1998). However, such a situation has not yet been observed.

The course of succession after a large-scale die-off of mature stands, therefore, does not proceed according to the classic doctrine: i.e., first, a preliminary or an initial forest, consisting of pioneer tree species, becomes established; then it is supplemented by the climax tree species (transition forest); and subsequently develops into a climax forest (Leibundgut 1978, Korpel 1995). Mountain ash in the regeneration layer of mature stands grows more quickly than Norway spruce. However, they are usually very far apart or are completely missing over large areas so that it is not possible to speak of an initial forest.

Consequently, the course of forest succession as described here concurs only to a certain degree with proposed models for secondary succession. In the montane Norway spruce forest – with the exception of a small percentage of European beech – neither pioneer and climax species, nor light and shade dependent species, can be clearly distinguished from one another. In this system, the role of Norway spruce is dual: it serves simultaneously as a pioneer as well as a climax tree species. In most of the area, mountain ash does not generate a classic initial forest; it only grows in association with Norway spruce. In this case, the classical succession models lose their validity. The future dynamics of the development of the ecosystem will probably also be determined primarily by Norway spruce. This is further based on the fact that the life expectancy of mountain ash is only about half that of Norway spruce (Korpel 1995).

The work of Jehl (2001) showed that the distribution of, and changes in, small-scale structural variables are highly responsible for determining the distribution of forest regeneration and are the reason for its aggregated occurrence. Regeneration is concentrated in favourable, small-scale locations. At such sites, as many as 16 plants larger than 10 cm in height were counted per square meter, while the grass-covered areas in the immediate vicinity were practically void of regeneration. "Hot spots" of regeneration are still found on old, decaying, fallen trunks and in areas close to dead trees. Heurich (2001) was able to show that 45% of all regeneration is found on or in the immediate vicinity of dead wood. This finding was not new: other authors also documented the positive effects of dead wood on forest regeneration in subalpine stands (Zierl 1972, Stoeckli 1995, Ott et al. 1997, Reif & Przybilla 1998, Jonášová 2004).

The present distribution of these local structures was pre-determined primarily by the earlier work of foresters in the mature forests. The classic linear regeneration on fallen trunks, which would have countered this pre-determination, occurs only to a very limited degree because fallen timber was consistently removed from the forest in former years. The small clusters and hordes of saplings will grow up together, support each other, and form a "fighting unit". Soon they will develop their own microclimates and will shade out any competition.

Influence of insects, fungi, and deer on forest regeneration

On the whole, only very little damage to young plants was registered. Fears that the Norway spruce bark beetle might be able to cause a large-scale die-off among the young trees have not been confirmed. So far, such damage occurred only in the Lusen area in 1997 after the large contiguous mature stands in that area had died off and the beetles – in their search for new food sources – infested young Norway spruce, thereby killing them as well.

Although it is not unusual to find bore holes in the branches of young plants of the natural regeneration, damages caused by weevils in the study area are practically insignificant. Fears that these beetles might be able to reproduce just as successfully in the root systems of dead trees as they do in the trunks of recently killed trees have not been confirmed. In contrast to the observations in the Rachel–Lusen area, many more weevils were registered in the Falkenstein–Rachel area, where trees infested by the Norway spruce bark beetle were removed (Bauer 2002).

March mushrooms (*Hygrophorus marzuolus*), which are described in the literature as one of the most important causes for the failure of regeneration (Ott et al. 1997, Schönenberger 1988, Brang 1996), have not yet been found in the sample plots. The reason for this may be the relatively high spring temperatures of the past several years, which have led to rapid melting of the snow cover. The fact that March mushrooms can have an important effect in the Bavarian Forest is documented by the massive losses of Norway spruce up to 2 m in height in the early 1980s (Scherzinger pers. comm.).

Probably because of the small size of the trees, the massive snow breakage events of the past two years did not result in much damage. Gnawing damage caused by mice was also insignificant.

Browsing damage to the main stem of Norway spruce occurs at a very low rate. However, the importance of browsing damage to the mountain ash, which is preferred by deer (Motta 2004), has increased in recent years. One problem is that most of the browsing damage to mountain ash in the subalpine range is caused in the summer and accumulates as the season progresses. As a result, the registered intensity of browsing damage to the main stems is dependent on the time of year in which an area is surveyed. The later in summer the measurements are made, the more browsing damage is likely to be registered. Since the inventories are usually carried out in early summer, browsing damage to the main stems is probably underestimated. It is assumed that the collapse of the old dead trees is forming such an intense entanglement, that the ability of ungulates to access the entire parts of area effectively is being inhibited. The result is a small-scale differentiation of the browsing damage situation (Hauser & Wittmann 2003). Contrary to this assumption, Kupferschmid & Bugmann (2005) were not able to detect any relationship between the tangle of deadwood and the amount of browsing damage. However, in addition to red deer, their study area also included chamois. The latter are still able to mover quite freely in spite of the jumble of broken trees.

The significance of disturbances for the development of the forest

The large-scale Norway spruce bark beetle outbreak is considered a so-called inherent disturbance since "the key organisms within the system are adapted to the effects of the disturbance" (Böhmer 1997). This implies that the ecosystem is highly flexible. The developments in the areas, in which the bark beetle had caused the massive die-off, have demonstrated that both mountain ash and Norway spruce are well adapted to such processes. Mountain ash, which cannot be infested by the Norway spruce bark beetle, "allows" its seeds to be dispersed by animals, produces fruit very early in the year, and is adapted to the extreme climatic conditions of the open areas. Norway spruce, a typical species of the boreal forest, is also well adapted. It possesses airborne seeds, which make it possible for the species to re-colonise even large disturbed areas. After a mast year in Switzerland, for example, Lässig et al. (1995) were able to detect ten Norway spruce seeds per square meter in an area that was 1000 m away from the next Norway spruce stand. Furthermore, Norway spruce is capable of germinating even on the thickest humus layers, is frost resistant, and can cope well with the climate of the open areas.

Critical for the successful colonisation of the areas, however, is the blossoming frequency of the trees, which sometimes can be quite low. Bülow (1964) wrote about the rare events of full and poor masts, which in the Bavarian Forest, occur only twice in a human lifetime. In the montane forests of Switzerland, a full mast can be expected about every five years (Ott et al. 1997). Even though an increased incidence of masts has been observed in the Bavarian Forest over the past several years, the frequency of fructification has an important influence on the rate of forest regeneration in a disturbed area. If the trees had blossomed in 1998 instead of in 1995, the forest succession would probably have taken a completely different course. The young plants that were already present in the original stands would have continued to grow in the same way, but the influx of seeds into the areas would have been much lower because, by 1998, a large portion of the subalpine forests had already died off. Seed-bearing, mature trees were almost completely absent in the central areas. If the trees had blossomed before the die-off had begun, most of the seedlings would have died inside the dark and cool mature stands, as was documented in the mast years of 1988 and 1992. The low regeneration rates observed in the Rachel area may also be attributed to the closed stands that were prevalent during the mast of 1995 and during the germination of the seedlings in the following year, when the conditions for growth of the seedlings were not favourable. After the mast of 2002, the regeneration densities in these areas may also be expected to increase.

According to these observations, the development and subsequent appearance of the forest is highly coincidental. But is forest development really only a matter of coincidence? A fascinating observation is that Norway spruce cone production and the explosive reproduction of the Norway spruce bark beetle appear to be closely correlated. Advantageous conditions for the population development of the Norway spruce bark beetle are also advantageous for the production and development of Norway spruce blossoms. When, after warm years with a sufficient water supply, the nutrient deposits of the trees are filled (Rohmeder 1972), the blossoming of Norway spruce is stimulated by the high temperatures and increased amount of sunlight in late June to early July. This is the time in which the female blossoms are produced. The trees blossom in the following year. Dry, warm weather conditions are advantageous for the further development of the cones (Schmidt-Vogt 1991). In spite of a full mast, ripe seeds cannot be produced in cold summers (Ott et al. 1997). Beudert (pers. comm.) was able to find a correlation between the climatic conditions in the Bavarian Forest in June and July of the respective preceding year on Norway spruce cone production in the years 1988, 1992, 1995, and 2002.

The beetle population also requires warm, dry years in order to cumulate in mass reproduction. Especially important is a warm spring. The beetles do not swarm until temperatures increase beyond 16–20°C. Therefore, it is not surprising that the 1995 blossom occurred at the "right" time: good beetle years are usually also good years for cone production.

Another indication of the reciprocal adaptation between the Norway spruce bark beetle and the Norway spruce is the fact that the pubescence (earliest ability to bear seeds) of Norway spruce occurs at an age of 30 to 40 years for free standing trees and 50 to 60 years for trees in closed stands (Rohmeder 1972). The Norway spruce bark beetle infests stands up to 70 years in age only if the densities are very high and (almost) does not invade stands younger than 50 years old (Becker & Schröter 2000). Because of this "co-ordination" Norway spruce are able to produce seeds before it becomes possible for the Norway spruce bark beetle to kill them off.

Therefore, the continuous co-evolutionary interaction between the antagonistic species Norway spruce bark beetle and Norway spruce has created a complex association between the two species. This relationship assures the survival of both (Cockburn 1995).

Consequences for National Park Management

An important goal for park management is designated in § 14(2) of the National Park Ordinance: "if the natural regeneration of the forest should fail over large areas and long periods of time, measures will be taken to support the development of a forest appropriate for the location and with a natural composition". Due to the considerable increase in regeneration densities, to currently 4502 plants per hectare, the situation has improved significantly since the 1990s. This is especially true when it is considered that most of the additional 738 plants per hectare that are now between 10 and 20 cm will have grown beyond the 20 cm threshold by the time of the next inventory. The average values have already reached levels that are recommended for low-altitude commercial forests. Values recommended by Burschel & Huss (1997), for example, are between 2000 and 5000 Norway spruce per hectare. The recommended values of Ott et al. (1997) of 1200 to 1800 for subalpine forests are even surpassed. Mayer & Ott (1991) even considered 200 young plants per hectare sufficient in order to secure the structural integrity of Norway spruce stands. Compared with primeval Central European Norway spruce forests, the regeneration densities attained in 2005 were also relatively high. Korpel (1995) reports an average of 600–800 plants in the primeval forests of the West Carpathian Mountains. Leibundgut (1978) states that densities above 2000 plants per hectare are rarely found in primeval montane forests.

It must be noted, however, that the regeneration is distributed quite unevenly throughout the subalpine range. This means that there are still areas with relatively few young plants. It is also important to remember that the majority of the plants are still very small and that much of the regeneration might still succumb to other "pests" in the future, such as March mushrooms (*Hygrophorus marzuolus)*. Plants cannot truly be considered secure until they have reached a height that is distinctly above that of the usual snow cover, which is 2–3 m (Ott et al. 1997).

It will take some time before the plants reach this size. Regeneration periods at subalpine altitudes are extremely long. According to Korpel (1995), the regeneration phase lasts up to 90 to 100 years. According to Mayer & Ott (1991) it may even extend to 100 to 200 years. Even for commercial forests, Ott et al. (1997) propose regeneration periods of over 150 years. The development of the regeneration in the study area, which is quite rapid for a montane forest ecosystem, leads to the assumption that the regeneration stage in a major portion of the subalpine range of the Bavarian Forest National Park will be completed much more rapidly.

Based on the present situation, it is not necessary to commence with artificial measures to support the natural regeneration of the forest. However, it will remain important to closely observe the development of the newly emerging forest in the future. This presents a great opportunity for the scientific documentation of this unique development and for the fulfilment of the political mandate.

References

Ammer C., 1998: Die Fichte in der natürlichen Verjüngung des Bergmischwalds. *Allgemeine Forst Zeitschrift*, 53: 396–399.

Bauer M., 2002: Walddynamik nach Borkenkäferbefall in den Hochlagen des Bayerischen Waldes. Ms., Dissertation, Technischen Universität München, 167 pp.

Bayerisches Staatsministerium für Ernährung Landwirtschaft und Forsten, 1982: Richtlinien für die mittel- und langfristige Forstbetriebsplanung in der Bayerischen Staatsforstverwaltung. Bayerisches Staatsministerium für Landwirtschaft und Forsten. München. 34 pp.

Becker T. & Schröter H., 2000: Ausbreitung von rindenbrütenden Borkenkäfern nach Sturmschäden. *Allgemeine Forst Zeitschrift*, 55: 280–282.

Brang P., 1996: Experimentelle Untersuchungen zur Ansamungsökologie der Fichte im zwischenalpinen Gebirgswald. *Beihefte zur Schweizerischen Zeitschrift für Forstwesen*, 77: 1–25.

Böhmer H.J., 1997: Zur Problematik des Mosaik-Zyklus-Begriffes. *Natur und Landschaft*, 72: 333–338.

Bülow G.V., 1964: Fichtennaturverjüngung in den Hochlagen des Bayerischen Waldes. *Allgemeine Forst Zeitschrift*, 19: 593–596.

Burschel P. & Huss J., 1997: *Grundriss des Waldbaus*. Paul Parey Verlag. Berlin & Wien, 478 pp.

Cockburn A., 1995: *Evolutionsökologie*. Gustav Fischer Verlag, Stuttgart, Jena & New York, 357 pp.

Fischer A., Abs G. & Lenz F., 1990: Natürliche Entwicklung von Waldbeständen nach Windwurf. Ansätze einer „Urwaldforschung" in der Bundesrepublik. *Forstwissenschaftliches Zentralblatt*, 109: 309–326.

Fischer A. & Jehl H., 1999: Vegetationsentwicklung auf Sturmwurfflächen im Nationalpark Bayerischer Wald aus den Jahren 1983. In: Forstliche Forschungsberichte. *Schriftenreihe der Forstwissenschaftlichen Fakultät der Technischen Universität München und der Bayerischen Landesanstalt für Wald und Forstwirtschaft*, 176: 93–101.

Grünvogel H. & Heurich M., 2002: Waldinventur 2002. Inventuranweisung. Nationalparkverwaltung Bayerischer Wald, Grafenau, 20 pp.

Hauser D. & Wittmann M.F., 2003: Der Einfluss von Totholzverhau auf einer ungeräumten Windwurf-Borken-

käferfläche auf Raumnutzung und Verbiss durch Rothirsche. Ms., Diplomarbeit, Fachhochschule Weihenstephan, Freising, 124 pp.
HEURICH M., 2001: Waldentwicklung im hochmontanen Fichtenwald nach großflächigem Buchdruckerbefall im Nationalpark Bayerischer Wald. In: Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall. *Nationalpark Bayerischer Wald, Wissenschaftliche Reihe*, 14: 99–176.
HEURICH M. & RALL H., 2006: Hochlageninventur 2005 und Luftbildauswertung 2003 bis 2005. Ergebnisse der Untersuchungen zur Waldentwicklung im Nationalpark Bayerischer Wald. *Berichte aus dem Nationalpark*, 3/2006, 20 pp.
HILDEBRAND K. & ROSENBERG A., 1996: Hinweise zum höhenzonalen Wachstum und Ökotypen der Vogelbeere. *Forst und Holz*, 51: 216–220.
HOHENADL W., 1981: Untersuchungen zur natürlichen Verjüngung des Bergmischwaldes. Dissertation, Forstwissenschaftliche Fakultät Universität München, 197 pp.
HOHMANN M. & ENGELS F., 1991: Was kommt nach dem Sturm? *Allgemeine Forst Zeitschrift*, 46: 630–633.
JEHL H., 1995: Die Waldentwicklung auf Windwurfflächen im Nationalpark Bayerischer Wald. In: *Nationalpark Bayerischer Wald – 25 Jahre auf dem Weg zum Naturwald*. Nationalparkverwaltung Bayerischer Wald, Grafenau, 88–112.
JEHL H., 2001: Die Waldentwicklung nach Windwurf in den Hochlagen des Nationalparks Bayerischer Wald. In: Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall. *Nationalpark Bayerischer Wald, Wissenschaftliche Reihe*, 14: 49–98.
JONÁŠOVÁ M. & PRACH K. 2004: Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak. *Ecological Engineering*, 23: 15–27.
KORPEL S., 1995: *Die Urwälder der Westkarparten*. Gustav Fischer, Stuttgart, 310 pp.
KUPFERSCHMID A., 2003: Succession in a protection forest after picea abies die-back. Ph.D. Thesis No. 15228, Swiss Federal Institute of Technology Zürich, 231 pp.
KUPFERSCHMID A. & BUGMANN H., 2005: Effect of microsites, logs and ungulate browsing on *Picea abies* regeneration in a mountain forest. *Forest Ecology and Management*, 205: 251–265
KUPFERSCHMID A., SCHÖNENBERGER W. & WASEM U., 2002: Tree regeneration in a Norway spruce snag stand after tree die-back caused by *Ips typographus*. *Forest Snow and Landscape Research*, 77: 149–160.
LÄSSIG R. & SCHÖNENBERGER W., 1993: Forschung auf Sturmschadensflächen in der Schweiz. *Forst und Holz*, 48: 244–249.
LÄSSIG R., EGLI S., ODERMATT O., SCHÖNENBERGER W., STÖCKLI B. & WOHLGEMUTH T., 1995: Beginn der Wiederbewaldung auf Windwurfflächen. *Schweizer Zeitschrift Forstwesen*, 146: 893–911.
LEIBUNDGUT H., 1978: *Europäische Urwälder der Bergstufe*. Verlag Paul Haupt, Bern & Stuttgart. 308 pp.
MAYER H. & OTT E., 1991: *Gebirgswaldbau – Schutzwaldpflege*. Gustav Fischer Verlag, Stuttgart & New York, 2. Auflage, 587 pp.
MOTTA R., 2003: Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. *Forest Ecology and Management*, 181: 139–150.
NÜSSLEIN S., 1998: *Waldentwicklung im Nationalpark Bayerischer Wald 1998. Totholzflächen und Waldverjüngung*. Bayerische Landesanstalt für Wald und Forstwirtschaft. Freising, 24 pp.
OTT E., FREHNER M., FREY H.U. & LÜSCHER P., 1997: *Gebirgsnadelwälder. Ein praxisorientierter Leitfaden für eine standortgerechte Waldbehandlung*. Haupt, Bern, Stuttgart & Wien, 287 pp.
PERRY D.A., 1997: Disturbance, recovery and stability. In: *Creating a forestry for the 21st century: the science of ecosystem management*. Island Press, Washtington D.C., 31–56.
RALL H., 1995: Die Wälder im Nationalpark Bayerischer Wald: Von forstwirtschaftlicher Prägung zur natürlichen Entwicklung. In: *Nationalpark Bayerischer Wald – 25 Jahre auf dem Weg zum Naturwald*. Nationalparkverwaltung Bayerischer Wald, Grafenau, 9–57.
REIF A. & PRZYBILLA M., 1998: Regeneration der Fichte in den Hochlagen des Nationalparks Bayerischer Wald. *Allgemeine Forst Zeitschrift*, 53: 400–403.
ROHMEDER E., 1972: *Das Saatgut in der Forstwirtschaft*. Verlag Paul Parey, Hamburg & Berlin, 273 pp.
ROMME W.H. & DESPAIN D.G., 1989: The Yellowstone Fires. *Scientific American*, 261: 37–46.
RYKIEL E.J., COULSON R.N., SHARPE P.J., ALLEN T.F.H. & FLAMM R.O., 1988: Disturbance Propagation by Bark Beetles as an episodic Landscape Phenomenon. *Journal of Landscape Ecology*, 1: 129–139.
SCHMIDT-VOGT H., 1991: *Die Fichte, Band II/3*. Verlag Paul Parey, Hamburg & Berlin, 647 pp.
SCHÖNENBERGER W., 1988: Die Überlebensraten in der Versuchsaufforstung Stillberg. *Schweizerische Zeitschrift für Forstwesen*, 139: 800–805.
SCHÖNENBERGER W., 2002: Post windthrow stand regeneration in Swiss mountain forests: the first ten years after the 1990 storm Vivian. *Forest Snow and Landscape Research*, 77: 61–80.
STOECKLI B., 1995: Moderholz für die Naturverjüngung. *Wald und Holz*, 76: 8–12.
TURNER, M.G., DALE V.H. & EVERHAM E.H., 1997: Fires, Hurricanes, and Volcanoes: Comparing Large Distur-

bances. *BioScience*, 47: 758–768
WERMELINGER B., DUELLI P., OBRIST M., ODERMATT O. & SEIFERT M., 1995: Die Entwicklung der Fauna auf Windwurfflächen mit und ohne Holzräumung. *Schweizerische Zeitschrift für Forstwesen*, 146: 913–928.
ZIERL H., 1972: Der Hochwald. Forstwissenschaftliche Forschungen. *Beihefte zum Forstwissenschaftlichen Zentralblatt*, 33: 1–80.

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