UNIVERSITY OF SOUTH BOHEMIA
Faculty of Science

Master Thesis

Evaluation of Spruce Forest Regeneration and Vegetation Changes

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Annotation:

The impact of a bark beetle outbreak, and the following sanitation management actions, on the mountain spruce forest in the central part of the Šumava Mountains were compared after twelve years of development. The survey was focused on natural regeneration of trees and herb-layer vegetation.

Anotace:

Porovnání vlivu žíru lýkožrouta a následné asanace na horské smrkové lesy v centrální části Šumavy po 12 letech vývoje. Výzkum byl zaměřen na přirozenou obnovu dřevin a bylinné patro.

Prohlašuji, že svoji diplomovou práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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Srdečně děkuji všem, kteří přímou i nepřímou podporou dopomohli ke vzniku a dokončení této práce. Jmenovitě patří můj dík Martinu Haisovi, Magdě Jonášové Edwards, Keithovi Edwards, Stanislavu Grillovi, Petru Šmilauerovi, Milanu Štechovi, Liboru Ekrtovi, Martinu Lepšímu, Aleně Jírové, Vaškovi Pouskovi; dále pak mojí rodině a přátelům.

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Chapter I: General introduction

1.1 Forest dynamics and disturbance regimes

Stability and dynamics of forest ecosystems

Until the early 1970s, natural forests were viewed as relatively balanced systems with predictable successional development leading to an equilibrium and endogenously self-replacing stage of forest development called climax (Clements, 1916); though, this concept overemphasized the stability of forest ecosystems (Kulakowski and Bebi, 2004; Kuuluvainen, 2002).

After the decades of ecological debates the reality of forest ecosystem functioning seems to be more complex (Frelich, 2002). Ecosystem change is regarded as the norm and natural disturbances are considered to be key ecological processes in almost all ecosystems (Attiwill, 1994; Kulakowski and Bebi, 2004; Kuuluvainen, 2002; Lindenmayer et al., 2008). Natural disturbance is "*an event (more or less discrete in time) that causes mortality of the dominant vegetation, thereby altering habitat and releasing resources*" (Lindenmayer et al., 2008). Disturbance processes can exist at overlapping temporal and spatial scales in a continuum (Frelich, 2002). Thus, the forest stability is currently viewed as a question of time and space scale, affecting the age structure and species composition. Hence, it is important to define the relevant scales at which the stability could exist (e.g., landscape 1000-1000 000 ha, stand 1-10 ha, or neighbourhood 0.01-0.1 ha) (Frelich, 2002). For example, forest stands develop after disturbances through developmental (physiognomic) stages: “stand initiation”, “stem exclusion”, “understory reinitiation”, and “old growth” at the stand scale (Oliver, 1981). And although stand-replacing disturbances initiate a new sequence of stand development, it does not have to be accompanied by changes in species composition (Frelich, 2002).

Disturbance regimes and forest landscape structure

Disturbances in forests vary spatially and temporally from frequent, low-intensity, gap-forming disturbances at the scale of neighbourhoods and individual trees to infrequent, high-intensity events at the scale of landscape that can significantly alter forest structure (Lindenmayer et al., 2008). In fact, disturbances can occur simultaneously at different scales, so the view of a hierarchical multiscale phenomenon could be more realistic (Kuuluvainen, 2002). The dynamics of disturbances interacts with many factors, such as climate, geomorphology, soils, species composition of forest and other factors (Kuuluvainen, 2002; Waring and Running, 2007). Accordingly, disturbance types and their characteristics (e.g., disturbance agents, intensity, severity, extent, frequency or others) combined for a given forest landscape result in the disturbance regime (Frelich, 2002; Lindenmayer et al., 2008). Disturbance regimes have ranges of their historical variability for a particular region and in turn form the species composition and structure of forests (Frelich, 2002). They determine proportions of stands of various stages of development on the landscape level. For example, since the stands are not predisposed to extensive blowdown until particular age (the late stem exclusion or understory reinitiation phase; what observed also Brůna et al. (2013) and Čada et al. (2013) in stands of the mountain spruce forests in Šumava Mts. ages over approximately 150 years are highly susceptible to disturbance), the effect of strong winds will have impact only on some of the forest stands (Frelich, 2002). On a lower level of hierarchy, neighbourhood effects between tree species interact with disturbances to structure the landscape patch mosaic (Frelich, 2002).

Responses of forest ecosystems to disturbances

As a stand experiences a series of disturbances that gradually increase in severity (what relates also to frequency), according to Frelich and Reich (1998), stand composition must necessarily change at some point. They modelled (for the boreal forests of the eastern North America) three possible responses of post-disturbance stand composition to disturbance severity: continuous; discontinuous; and cusp response. These responses can be linked with the type of neighbouring effects among individual trees in a community to a three-dimensional surface. The surface can describe the response of species composition (early- to late- successional species) as a function of both disturbance severity (low to high) and type of neighbouring effects (positive, neutral, negative; exerted by the dominant species in a forest stand) that determines the trajectory of the response for the community (Frelich, 2002). The response to disturbance may be linear or non-linear, and it corresponds to the type of neighbourhood effects (Frelich, 2002). Consequently, the stands dominated by species with strong positive neighbourhood interactions (such species promote their self-replacement) change composition of species only if the disturbance is severe enough. Otherwise, the original tree species regenerate in such stand after a disturbance. For instance, the response to cumulative disturbance effects for late-successional stands could be that if disturbances remove either the understory layer or the overstory layer, stand composition could remain the same, while removal of both the understory and overstory layers could cause replacement by early-successional species (Frelich, 2002).

Historical range of variability of mountain spruce forests in Central Europe

Majority of coniferous forest ecosystems belong to a mosaic of vegetation types of the boreal forest (taiga), spreading over the vast areas in the high latitudes of northern hemisphere (Bonan and Shugart, 1989). The mountain coniferous forests in Central Europe represent similar type of ecosystem, occurring to a lesser extent outside the boreal zone in the higher altitudes where similarly harsher conditions of climate let the conifers to dominate over deciduous tree species (Moravec, 1994). Nevertheless, disturbance regimes of Norway spruce (*Picea abies* (L.) Karst.) likely differ among different geographical regions within boreal geographical zone (Kuuluvainen, 2002) and also between boreal FennoScandia and temperate Central Europe, e.g., due to different proportions of disturbance agents (Svoboda and Pouska, 2008).

The major disturbance agent in Central European mountain spruce forests is wind (Schelhaas et al., 2003). There is usually a high correlation between damage by strong winds and by bark beetle (mainly *Ips typographus* (L.)) outbreaks (Schelhaas et al., 2003). Large windthrows of spruce stands together with dry warm weather in the beginning and during the growing season likely result in bark beetle outbreaks and die back of spruce stands (Grodzki et al., 2006; Schelhaas et al., 2003). The relations have been recently observed in the bark beetle outbreaks along Germany-Czech border in the Bayerischer Wald (since 1983, 1984: e.g., Fischer et al., 2002; Heurich et al., 2001) and the Šumava Mts. (since 1990s: e.g., Hais et al., 2009; Jonášová and Prach, 2004; Svoboda et al., 2012), along Slovak-Polish border in the Tatra Mts. (1993-1998: Grodzki et al., 2006; and since 2004: Jonášová et al., 2010), or in the Swiss Alps (since 1990s: Kupferschmid and Bugmann, 2005).

In the last few years, several studies from Central Europe and especially from the Šumava Mts. dealt with reconstructions of disturbance history to shed more light on the range of historical variability for the forest ecosystems in the region as traditional views considered the large disturbances only as unnatural and happening nowadays due to previous forestry practices (Svoboda et al., 2012). In a semi-natural montane spruce forest in the southern part of the Šumava Mts. near the Trojmezná Mt., Svoboda et al. (2010) observed a prolonged recruitment period spanning seven decades since the late 1800s when the early stand development was affected by the combination of successive events: establishment of advance regeneration, windstorms, bark beetle outbreak, and salvage logging. Detected periods correspond with the well-known high-severity windthrows from 1868, 1869, and 1870 and subsequent bark beetle outbreaks followed by extensive salvage logging in that times (Brůna et al., 2013); and other outbreaks after the Second World War (Schelhaas et al., 2003). In the northern part of the Šumava Mts. at the Jezerní hora Mt., Čada et al. (2013) identified both high-severity and also less severe disturbances, also consistent with other records from the Šumava Mts. Time intervals of severe windstorms that initiated new stand development were inferred between reconstructed (1820s and 1860s) and present windstorms to 150 and 190 years (Čada et al., 2013). Finally, the landscape-level study in both the Šumava Mts. and the Bayerischer Wald revealed significantly changed age structure as a result of severe disturbances; what indicated that recent bark beetle outbreak (1990s) occurred in even-aged stands in the approximate age of 130 years that covered extensive areas after the historical disturbances from late 1800s and due to their age were susceptible to disintegration (Brůna et al., 2013). Despite the recurrent severe disturbances, the old-growth forests are within historical range of variability at the landscape-scale (Brůna et al., 2013). In conclusion, historical range of variability of mountain spruce forests in Central Europe comprises continuum from the small-scale gap dynamics to large-scale, high-severity disturbances occurring at various temporal and spatial scales; unlike the previously accepted view that dynamics is driven only by gap dynamics of small cycle with endogenous tree mortality (Svoboda et al., 2012).

1.2 Legacies of natural disturbances versus post-disturbance logging

Biological legacies of natural disturbances and their consequences

In mountain spruce forest of the Šumava Mts., strong winds causing the large-scale windthrows and bark beetle outbreaks provide the heterogeneity on the landscape scale as each produce its typical physical and organic structures on the stand scale and as some stands are affected while the others stay untouched during an event (Foster and Orwig, 2006; Kulakowski and Bebi, 2004). In turn, such landscape heterogeneity increases the likelihood that future disturbances will not affect the whole area (Kulakowski and Bebi, 2004). At the stand scale, the structures and organisms that disturbances leave behind are called biological legacies. They include windthrown trees, standing dead trees, living trees, intact understory vegetation or whole undisturbed refugia, depending on the disturbance event (Frelich, 2002; Lindenmayer et al., 2008). Therefore, the effective size of disturbance depends less on the disturbance perimeter or area as the placement of surviving individuals is of higher importance for recovery of particular species (Frelich, 2002; Romme et al., 1998) and although these disturbances are often considered as stand-replacing events, it relates mainly to removal of former canopy of mature trees than to decline of species (Frelich, 2002).

As a consequence of disturbances, the mortality of mature spruce trees is increased but they rejuvenate the system and help to maintain or increase its long-term productivity (Attiwill, 1994; Christiansen et al., 1987; Waring and Running, 2007) by enhanced nutrient cycling (Kaňa et al., 2012; Svoboda et al., 2006). Light conditions are changed in comparison to live canopy depending on disturbance agent. In case of bark beetle outbreak, however, the change is slow because dead standing trees gradually lose foliage, fine branches, larger branches, and finally portions of boles (Lindenmayer et al., 2008).

In general, many species are favoured by the opened canopy or habitats created by disturbances, such as dead wood (Lehnert et al., 2013; Lindenmayer et al., 2008; Müller et al., 2008). Among them, wood-decaying fungi play an essential role for the functioning of forest ecosystem as they provide habitats for other species in the dead wood (including spruce regeneration), are involved in nutrient cycling, and soil formation (Lonsdale et al., 2008), while their occurrence is influenced by the properties of the wood they occupy and their diversity relates to coarse woody debris of different stages of decay, sizes, but also causes of tree death (Pouska et al., 2011). For example, although some of the currently bark beetle affected spruce forests in the Šumava – Bayericher Wald National Parks possess lots of relatively fresh dead wood, they are less diverse than old-growth stands as a result of wood removal in the past (Bässler et al., 2012). Nevertheless, dead standing trees provide the favourable niche for, e.g., *Fomitopsis pinicola* that decays the snags and causes their fall after 5-10 years, while this type of rot increased the presence of red-listed *Androdiella citrinella* (Bässler and Müller, 2010; Pouska et al., 2011).

Consequences of post-disturbance management practices

As other post-disturbance management practices, salvage logging is a widespread practice after the stand-replacing natural disturbances, which has strong negative impacts on ecological processes depending on how it is conducted (Lindenmayer et al., 2008). In the

Šumava National Park, sanitation fellings (tree removal to limit the spreading of bark beetle) and salvage logging (tree removal to recover the economic value; Lindenmayer et al., 2008) have been applied simultaneously and mainly in the form of clearcutting. Such operations cause an additional anthropogenic disturbance that occurs shortly after the natural disturbance and increases its severity (Frelich and Reich, 1998). As a result, the effect on the forest ecosystem is greater – than that of the natural disturbance itself – to which organisms do not have to be adapted (Foster and Orwig, 2006; Lindenmayer and Noss, 2006).

Populations of organisms, including their species composition, the stand structure, and ecosystem processes are affected by logging; usually negatively and their outcomes reach beyond the first tree generation (Lindenmayer et al., 2008). Natural vegetation recovery is impaired as advance tree regeneration and understory herb and moss layers are mechanically damaged during clearing operations (observed Jonášová and Prach, 2004) and in consequence suddenly exposed to changed light, water, and nutrients regime (Foster and Orwig, 2006; Lindenmayer et al., 2008), or other environmental conditions (Hais and Kučera, 2008; Hais et al., 2009). Moreover, the removal of all trees in affected stands during the bark beetle outbreak can have long-term genetic consequences because it removes also the individuals that would otherwise survive the attack and serve as beneficial sources of seeds (Lindenmayer et al., 2008). Moreover, applied replantings also do not have to be beneficial for the forest communities (avoidance of replantings suggested by Müller et al. (2008) to lengthen the important phase of sunlit conditions that favour insect diversity of mountain spruce forests in the Bayericher Wald National Park). Furthermore, many other benefits of natural disturbances, especially biological legacies are removed or eliminated, what destroys the habitats related to natural post-disturbance structure (Lindenmayer et al., 2004). The amount and type of biological legacies depends on the severity of disturbance (Frelich, 2002; Lindenmayer et al., 2008) that is higher in the case of clearcut in comparison to naturally disturbed forest (Lindenmayer et al., 2008). The negatives of missing legacies for future ecosystem functioning become apparent if one considers that probably majority of the pre-disturbance structures are legacies of events that occurred over 150 years ago (Svoboda et al., 2012), although some of them could develop also during the early stages of stand development after low severity disturbances (Brůna et al., 2013). In addition, salvage logging is among the most effective operations of bark beetle control but it opens fresh forest edges that consequently increase the susceptibility to new attacks of previously unaffected spruce trees (Grodzki et al., 2006). Such loggings may, thus, exceed the extent and intensity of the natural disturbance (Foster and Orwig, 2006), resulting in fragmentation of forest stands that limits the recovery of native species (Frelich, 2002). Considering all the above mentioned, the post-disturbance operations exceed the historical range of variability of disturbance regime in mountain spruce forests and impair the potential of natural disturbances to aid to recover the natural character of stands previously simplified by forest management (Jonášová and Prach, 2004; Kulakowski and Bebi, 2004; Lindenmater et al., 2004).

1.3 Regeneration of mountain spruce forest after the disturbances

Ability of forest ecosystems to regenerate

The existence of forest ecosystems prior to the human landscape management clearly demonstrated their ability to recover naturally (Lindenmayer et al., 2008). Organisms evolved life strategies and adaptations on particular types of physical and biotic environment and to types of disturbances within the historical range of variability (Waring and Running, 2007). The complex interactions among disturbance types and tree species determined the regeneration process after the event as some species can be able to regenerate within the disturbed area (e.g., seedling or soil seed banks) while others will need to arrive from outside (Frelich, 2002). In Central Europe, there are historical evidences of forest regeneration following large-scale disturbances of mountain spruce forest (e.g., Brůna et al., 2013; Čada et al., 2013; Svoboda and Pouska, 2008; Svoboda et al., 2010; 2012). These ecosystems proved to be highly flexible and adapted to the conditions of large-scale windtrows and bark beetle outbreaks (Heurich, 2009) as spruce trees coevolved with other organisms, what implies mutual dependencies between some organisms and also the mechanisms of defence and offense (Kimmins, 2004).

In mountain spruce forests in Central Europe, the coevolutionary interaction between the antagonistic species – bark beetle (*Ips typographus*) and Norway spruce (*Picea abies*) – works to maintain the forest ecosystem: while bark beetle predominantly attacks spruce individuals that are old or otherwise weakened, it is able to cause a die-back of relatively healthy trees during its outbreak (Christiansen et al., 1987). However, massive cone production provide an additional supply of seeds before the spruce stands die-back as the weather conditions advantageous for bark beetle over-population favours also the reproduction of spruce (Heurich, 2009). Coincidence between a mast year and a die-back of the stand is followed by high numbers of freshly germinated spruce seedlings which majority survive the first years under the increased light conditions of opening canopy whereas their numbers decrease (as normally) if the mast year comes too early prior to the outbreak (Heurich, 2009; Jonášová and Prach, 2004).

In addition, organisms possess also the ability to adapt to changing conditions through favouring of the particular genotypes within population that are appropriate for the species (Kimmins, 2004). Spruce individuals that survive the disturbance benefit from reduced competition for light, water, and nutrients (Waring and Running, 2007), while they represent important source of seeds as they proved higher resistance and other seed sources may be limited in the early phase of post-disturbance regeneration of large-scale disturbed forest.

Progress of regeneration and the effect of microsites

The process of regeneration after the large-scale disturbances have yet not been completely clarified for mountain spruce forests in Central Europe as there were almost no spontaneously developing forests after the disturbances. Rather than *if the forests will regenerate*, the question is posed as *how will the regeneration proceed*. It is also the main question elaborated in the next chapter on the post-disturbance development of forests following the bark beetle outbreak since 1990s in the central part of the Šumava Mts. And the post-disturbance spontaneous development versus forestry intervention is compared.

The first studies of forest regeneration after the disturbances were enabled after some windthrows and consequent bark beetle outbreaks in non-intervention zones since late 1980s in the Bayericher Wald National Park (after bark beetle outbreak – Heurich et al., 2001; after windthrow – Jehl, 2001), since 1990s also in the Šumava NP (Jonášová and Prach, 2004) and in the Swiss Alps (Kupferschmid and Bugmann, 2005). Since then, the first stage of post-disturbance development shows that spontaneous regeneration of disturbed forests provides sufficient numbers of trees (mainly spruce) per hectare (with rather wide ranges) in the Šumava – Bayerischer Wald National Parks if the regeneration success is compared with the rules for commercial forests (Čížková et al., 2011; Heurich, 2009; Jonášová and Prach, 2004; Svoboda et al., 2010; Ulbrichová et al., 2006; etc.). However, such evaluation should not be anyway binding in the spontaneously developing areas of national parks and the observed wide range of seedling, sapling, and young tree densities could be rather welcomed to increase the heterogeneity on the land-scape level.

According to current knowledge, mountain spruce forests in the Central Europe seem to regenerate directly with the same species composition after the large-scale bark beetle outbreaks and the spruce regeneration dominates, while the rowan numbers were increased only temporary (e.g., Heurich, 2009; Jonášová and Prach, 2004). Unlike the expectations to follow the model of large-cycle after large-scale disturbances, there is not observed the change in species composition of initial forest that would be formed by pioneer species (Heurich, 2009; Jonášová and Prach, 2004). Norway spruce (*Picea abies*) seems to be midtolerant and plays a role in between a climax species and a pioneer species while rowan grows in the association with spruce (Żywiec and Ledwoń, 2008) but does not form the expected initial forest (Heurich, 2009; Whitmore, 1989). Therefore, pioneer/climax or light/shade-dependent species cannot be clearly distinguished from each other in these forests (Heurich, 2009). Similarly, the special case of waterlogged spruce forests in the Šumava Mts. was observed to be regenerated by the original tree species composition after the bark beetle outbreaks (Jonášová and Matějková, 2007; Vrška et al., 2001).

As the largest amounts of individuals were growing prior to the event, either as older saplings awaiting the changed light conditions under closed canopy or the high amounts of youngest seedlings that germinated after the pre-disturbance mast, the importance of post-disturbance legacies prove true also for forest regeneration (Čížková et al., 2011; Jonášová and Prach, 2004; Svoboda et al., 2010; Zielonka, 2006). The opened canopy is after large-scale disturbance followed by phase when the advanced regeneration is stimulated to substitute the previous canopy. Without the increased light conditions, previously high densities of seedlings decrease with the increasing height of individuals (as observed, e.g., Svoboda et al. (2010) in the semi-natural montane spruce forest in the Šumava Mts.).

In addition, structure of the tree layer before disturbance has the effect on the following stand development (Zenáhlíková et al., 2011) and also the common removal of dead wood in mountain spruce forests consequently influences the amounts of advance spruce regeneration in the next forest generation. Spruce regeneration is highly concentrated on uplifted surfaces like coarse woody debris – mainly to laying logs, stumps, or bases of standing mature spruces (living or snags); and although it covered only a small percentage of the soil surface, it harboured the largest portion of seedlings (Bače et al., 2009; 2012; Čížková et al., 2011; Heurich, 2001; 2009; Jonášová and Prach, 2004; Kupferschmid and Bugmann, 2005; Kupferschmid et al., 2006; Svoboda and Pouska, 2008; Svoboda et al. 2010; Zenáhlíková et al., 2011; Zielonka, 2006). Dead wood structures created by a disturbance event play many roles for decades for a variety of organisms as the decomposition advances and approximately in between 30 and 60 years after tree death become suitable substrate for the establishment of spruce seedlings (Zielonka and Piątek, 2004; Zielonka, 2006). Dead wood facilitates the survival of spruce seedlings and promotes their growth through many ways, e.g., moisture retention, mineral cycling, and provision of mycorrhizal fungi (Lonsdale et al., 2008). And the recruitment bank of spruce on logs is continuously renewed with new supply of seeds after the mast year (Bače et al., 2012; Zielonka, 2006). Nevertheless, considering the supply of dead wood in relation to recent bark beetle outbreak, such trees were decayed mainly by brown-rot-causing *Fomitopsis pinicola* that was found to be less appropriate for spruce seedlings; the exposition of logs to higher temperatures and moisture fluctuations can additionally explain lower densities of seedlings on this type of dead wood (Bače et al., 2012). Another favourable microsite for spruce is spruce litter while higher herb vegetation is rather unfavourable, especially for small seedlings (Čížková et al., 2011; Heurich, 2009; Jonášová and Prach, 2004). On the other hand, rowan does not seem to have such specific preferences to microsite, though the highest density was found around bases of thicker spruces (Bače et al. (2009) – the Šumava Mts.) near the edge of the stand gap as the seed-dispersing birds often perch to hide and consequently defecate (Żywiec and Ledwoń (2008) – the Polish Tatra Mts.).

The microsites created by particular disturbance can be suitable for different species. In contrast to spontaneously developing stand after the attack of bark beetle, windthrow offer more diverse habitats for colonization, pits and mounds (Schaetzl et al., 1989), where light-demanding or early-successional species (birch *Betula* spp.) can germinate in soil disturbed by uprooting of trees (Fischer et al., 2002; Ilisson et al., 2007; Jonášová et al., 2010; Ulanova, 2000). As a result, the regeneration progress may differ not only in windthrows and die-backed stands but also in clearcuts where soil surface is usually disturbed in higher extent (Fischer et al., 2002; Ilisson et al., 2007; Jonášová and Prach, 2004).

Comparison with regeneration after logging

It seems that after both bark beetle outbreak (Heurich, 2009; Jonášová and Prach, 2004) and in windthrows (as Fischer et al. (2002) observed), the regeneration proceeds without the change of communities of tree and herb species that formed the previous forest, unless the post disturbance interventions are applied. Not many studies were concerned in the comparisons of spontaneously developing stands after the die-back and additionally disturbed clearcuts. In the central part of the Šumava Mts., such comparisons have been enabled since 1997 when Jonášová and Prach (2004) established the long-term study of the regeneration processes. The first years of study showed the positive effect of dead canopy on the natural species composition with sufficient numbers of spruce and rowan. It contrasted with clearcut where the numbers of both spruce and rowan were lower and their height and age variability was reduced as the originally most numerous category of the youngest seedlings was eliminated (Jonášová and Prach, 2004). On the other hand, some pioneer trees as birch (*Betula* sp.), willow (*Salix* sp.), and aspen (*Populus tremula*) established (Jonášová and Prach, 2004). Windthrows followed by post-disturbance interventions were considered to have similarly negative conditions like cleared plots representing the highest level of changes (in the Šumava Mts., Jonášová and Matějková, 2007; or in Norway spruce dominated forests in Estonia, Ilisson et al., 2007).

Understorey vegetation

Similarly as the disturbance events condition the tree regeneration, they also affect the understory of mountain spruce forests (Holeksa, 2003); with the most intense changes caused by post-disturbance interventions (Jonášová and Prach, 2008). After the opening, the total amount of the herb vegetation increased in both dead wood stands and clearcuts, while the increase was lower and it started to decrease again in spontaneously developing stands since 2000 (after three years) due to falling tree branches and tree parts; unlike in clearcuts (Jonášová and Prach, 2004; 2008). In addition, species composition of herbs was also more changed in clearcuts that favoured competitive grasses and some pioneer species more than the spontaneously developing stands (Jonášová and Prach, 2008). The cover by mosses decreased after disturbances; and since they were more susceptible to the post-disturbance interventions than herbs, more decreased cover and also changed species composition of moss communities towards pioneer species were observed in clearcuts (Jonášová and Matějková, 2007; Jonášová and Prach, 2004; 2008). During the first years of development in the Bayerischer Wald National Park, Jehl (2001) similarly observed insignificant changes to herb layer but the significant decrease of moss layer in dead wood stands; and Fischer et al. (2002) the increase of pioneer species, mainly raspberry (*Rubus idaeus*) in the windthrown areas. Nevertheless, only minor changes in both herb and moss layers over time were observed in waterlogged spruce forests (Jonášová and Prach, 2008). In conclusion, spontaneously developing stands after the bark beetle outbreak possess snags that seem to have positive effects by partial shading and moderating the changes caused by canopy reduction while the clearcutting changes the understory more than the initial disturbance (Jonášová and Matějková, 2007; Jonášová and Prach, 2004; 2008).

1.4 Implications for management of national parks

Large reserves represent the best examples of ecosystems, what is also because they stayed relatively free of intense human impacts (Lindenmayer et al., 2008). As such, they enable survival of variety of organisms within the particular ecosystems and also those that are intolerant of human manipulation or intrusion (Lindenmayer et al., 2008). They also represent the control areas to get knowledge about natural processes and possibly to derive implications for managed forests (Lindenmayer et al., 2008). In similar sense, the objectives of the Šumava National Park are defined as: *"conservation and improvement of the environment; especially conservation or restoration of self-controlling ecological processes, strict conservation of the animals and plants, conservation of typical landscape, accomplishing of scientific and educational aims, together with utilization of the area for touristic and recreation in ways that do not impair the natural environment;"* and *"economic or other utilization of the national park have to be subordinated"* to its main objective (Nařízení vlády č. 163/1991 Sb.).

On the other hand, when national parks are confronted with natural processes, such as natural disturbances belong to, managers do not always adhere to the objectives with which the national parks were established (like in the Šumava National Park; and in Slovakian Tatranský Národny Park, Grodzki et al., 2006) and the ecological objectives are sometimes changed to economic ones with salvage logging, although the removal of timber would not otherwise been allowed (Lindenmayer et al., 2008). Traditional management practices are often applied to face the "calamity" and "enemies", such as bark beetle. Among reasons for this paradox belong the financial considerations, a fear of the die-back, and the common label of bark beetle as "a pest" that is deniably legitimate in commercial forestry but not in the forest ecosystems where it belongs to (Míchal and Petříček, 1999; as was also proved for the mountain spruce forests within the Šumava National park, discussed above – e.g., Svoboda et al., 2012). Other reasons include a desire to tidy up "the mess" after the disturbance and otherwise it is considered as wasting or a hazard to human safety (Lindenmayer et al., 2008).

The latter is, however, legitimate along path and not for the whole stands (Foster and Orwig, 2006). Hence, when sudden disturbance events occur, there is a tendency to manage the area as it would be commercial forest. Nevertheless, such forestry interventions to control bark beetle outbreaks seems to be at least equally effective as the effect of cold and rainy weather on spruce trees and bark beetle, possibly complemented with the increase in the activity of natural enemies of bark beetle (parasitoids, entomopathogens) when the total mortality of trees and time progress were considered by Grodzki et al. (2006) in the Tatra Mts.

However, post-disturbance salvage logging is generally inappropriate for national parks not only due to its broad negative consequences, whether the disturbance is considered to be within the historical range of variability for the ecosystem or to be of novel form (Lindenmayer et al., 2008); but also because forestry interventions are in serious disagreement with the sense and objectives of national parks, especially in zones of highest protection in national parks (Míchal and Petříček, 1999); they are, nevertheless, considerable for the buffering zones towards the commercial forests outside the park (as works for the Bayericher Wald National Park). Therefore, the salvage logging is controversial because it often results from nonobservance of pre-disturbance management objectives, although disturbances are not expected to automatically result in changes in the basic objectives of a forest (Lindenmayer et al., 2008). As an alternative to re-consideration of the objectives in selecting post-disturbance activities, better approach would be to integrate disturbances into management plans ahead as we have to accept that they will continue to occur (Lindenmayer et al., 2008; Kimmins, 2004; Schelhaas et al., 2003; Waring and Running, 2007).

In conclusion, leaving ecosystems to develop their way even after the large-scale disturbances in national parks is a good way to promote the biodiversity that was decreased in commercial forests elsewhere, as a case study from the Bayericher Wald NP supports (Lehnert et al., 2013). Non-intervention zones of ∼10,000 ha sustained variety of biological legacies of dense and early-successional forests, without a loss of species adapted to other stages (Lehnert et al., 2013). Besides, without enough large non-intervention zones, the Šumava National Park cannot be internationally accepted as "national park" (IUCN category II; Dudley, 2008). However, national parks in this sense are appropriate to get knowledge about natural ecosystem functioning, from which implications for commercial forests can be derived. For instance, Kuuluvainen (2002) suggest that natural disturbance dynamics should be used as a paradigm for ecological restoration and sustainable management of forests to support the biodiversity. Besides, managing ecosystems within the historical range of variability is supported by many authors (e.g., Attiwill, 1994; Kimmins, 2004; Kulakowski and Bebi, 2004; Kuuluvainen, 2002; Lindenmayer et al., 2006); what could be difficult to make it work, though (Frelich, 2002; Waring and Running, 2007). Nevertheless, based on the knowledge from mountain spruce forests in the Šumava Mts., sustainable management strategies should have more heterogeneous manner and include the continuum of natural disturbances and their biological legacies (Čada et al., 2013). Specifically, Čížková et al. (2011) suggested for post-disturbance forest management to consider advance regeneration that is present prior the natural disturbance and ensures forest recovery.

1.5 References

Attiwill, P.M., 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63, 247-300.

Bače, R., Janda, P., Svoboda, M., 2009. Vliv mikrostanoviště a horního stromového patra na stav přirozené obnovy v horském smrkovém lese na Trojmezné [Effect of microsite and upper tree layer on natural regeneration in the mountain spruce forest stand Trojmezná (Šumava National Park)]. Silva Gabreta 15, 67-84 (in Czech, English Summary).

Bače, R., Svoboda, M., Pouska, V., Janda, P., Červenka, J., 2012. Natural regeneration in Central-European subalpine spruce forests: Which logs are suitable for seedling recruitment? Forest Ecology and Management 266, 254-262.

Bässler, C., Müller, J., 2010. Importance of natural disturbance for recovery of the rare polypore *Antrodiella citrinella* Niemelä & Ryvarden. Fungal Biology 114, 129-133.

Bässler, C., Müller, J., Svoboda, M., Lepšová, A., Hahn, C., Holzer, H., Pouska, V., 2012. Diversity of wood-decaying fungi under different disturbance regimes – a case study from spruce mountain forests. Biodiversity and Conservation 21, 33-49.

Bonan, G.B., Shugart, H.H., 1989. Enviromental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics 20, 247-300.

Brůna, J., Wild, J., Svoboda, M., Heurich, M., Müllerová, J., 2013. Impacts and underlying factors of landscape-scale, historical disturbance of mountain forest identified using archival documents. Forest Ecology and Management 305, 294-306.

Čada, V., Svoboda, M., Janda, P., 2013. Dendrochronological reconstruction of the disturbance history and past development of the mountain Norway spruce in the Bohemian Forest, central Europe. Forest Ecology and Management 295, 59-68.

Christiansen, E., Waring, R.H., Berryman, A. A. 1987. Resistance of conifers to bark beetle attack: searching for general relationships, Forest Ecology and Management 22, 89-106.

Čížková, P., Svoboda, M., Křenová, Z., 2011. Natural regeneration of acidophilous spruce mountain forests in non-intervention management areas of the Šumava National Park – the first results of the Biomonitoring project. Silva Gabreta 17, 19-35.

Clements, F.E., 1916. Plant succession: An analysis of development of vegetation. Carnegie Institute Washington Publications 242, Washington, DC.

Dudley, N. (Ed.), 2008. Guidelines for Applying Protected Area Management Categories. IUCN. Gland, Switzerland. Available online, <www.iucn.org/publications>.

Fischer, A., Lindner, M., Abs, C., Lasch, P., 2002. Vegetation dynamics in Central European forest ecosystem (near-natural as well as managed) after storm events. Folia Geobotanica 37, 17-32.

Foster, D.R., Orwig, D.A., 2006. Preemptive and Salvage Harvesting of New England Forests: When Doing Nothing Is a Viable Alternative. Conservation Biology 20, 959–970.

Frelich, L.E., Reich, P.B., 1998. Disturbance severity and treshold responses in the boreal forest. Conservation Ecology [online] 2, 7. Available online, <http://www.consecol.org/vol2/iss2/art7/>.

Frelich, L.E., 2002. Forest Dynamics and Disturbance Regimes. Cambridge University Press, Cambridge.

Grodzki, W., Jakuš, R., Lajzová E., Sitková, Z., Maczka, T., Škvarenina, J., 2006. Effects of intensive versus no management strategies during an outbreak of the bark beetle *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) in the Tatra Mts. in Poland and Slovakia. Annals of Forest Science 63, 55-61.

Hais, M., Kučera, T., 2008. Surface temperature change of spruce forest as a result of bark beetle attack: remote sensing and GIS approach. European Journal of Forest Research 127, 327-336.

Hais, M., Jonášová, M., Langhammer, J., Kučera, T., 2009. Comparison of two types of forest disturbance using multitemporal Landsat TM/ETM+ imagery and field vegetation data. Remote Sensing of Environment 113, 835-845.

Heurich M., 2001. Waldentwicklung im montanen Fichtenwald nach großflächigem Buchdruckerbefall im Nationalpark Bayerischer Wald. In: Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall. Nationalpark Bayerischer Wald, Wissenschaftliche Reihe 14, 99-177 (in German, English Summary).

Heurich, M., 2009. Progress of forest regeneration after a large-scale *Ips typographus* outbreak in the subalpine *Picea abies* forest of the Bavarian National Park. Silva Gabreta 15, 49-66.

Heurich, M., Reinelt, A., Fahse, L., 2001. Die Buchdruckermassenvermehrung im Nationalpark Bayerischer Wald. In: Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall. Nationalpark Bayerischer Wald, Wissenschaftliche Reihe 14, 9-48 (in German, English Summary).

Holeksa, J., 2003. Relationship between field-layer vegetation and canopy openings in a Carpathian subalpine spruce forest. Plant Ecology 168, 57-67.

Ilisson T., Köster K., Vodde F., Jõgiste K. (2007): Regeneration development 4-5 years after a storm in Norway spruce dominated forests, Estonia. Forest Ecology and Management 250, 17-24.

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 (in German, English Summary).

Jonášová, M., Matějková, I., 2007. Natural regeneration and vegetation changes in wet spruce forests after natural and artificial disturbances. Canadian Journal of Forest Research 37, 1907-1914.

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.

Jonášová, M., Prach, K., 2008. The influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests. Biological Conservation 141, 1525-1535.

Jonášová, M., Vávrová, E., Cudlín, P., 2010. Western Carpathian mountain spruce forest after a windthrow: Natural regeneration in cleared and uncleared areas. Forest Ecology and Management 259, 1127-1134.

Kaňa, J., Tahovská, K., Kopáček, J., 2012. Response of soil chemistry to forest dieback after bark beetle infestation. Biogeochemistry 113, 369-383.

Kimmins, J.P., 2004. Forest Ecology: A Foundation for Sustainable Forest Management and Environmental Ethics in Forestry, third ed. Prentice Hall, Upper Saddle river, New Jersey.

Kulakowski, D., Bebi, P., 2004. Range of Variability of unmanaged subalpine forests. Forum für Wissen 2004, 47-54.

Kupferschmid, A.D., Brang, P., Schönenberger, W., Bugmann, H., 2006. Predicting tree regeneration in *Picea abies* snag stands. European Journal of Forest Research 125, 163-179.

Kupferschmid, A.D., 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.

Kuuluvainen, T., 2002. Natural Variability of Forests as a Reference for Restoring and Managing Biological Diversity in Boreal Fennoscandia. Silva Fennica 36, 97-125.

Lehnert, L.W., Bässler, C., Brandl, R., Burton, P.J., Müller, J., 2013. Conservation value of forests attacked by bark beetles: Highest number of indicator species is found in early successional stages. Journal for Nature Conservation 21, 97-104.

Lindenmayer, D.B., Burton, P.J., Franklin, J.F., 2008. Salvage logging and its ecological consequences. Island Press. Washington.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A., Perry, D., 2004. Salvage Harvesting Policies After Natural Disturbance. Science 303, 1303.

Lindenmayer, D.B., Noss, R.F., 2006. Salvage Logging, Ecosystem Processes, and Biodiveristy Conservation. Conservation Biology 20, 949-958.

Lonsdale, D., Pautasso, M., Holdenrieder, O., 2008. Wood-decaying fungi in the forest: conservation needs and management options. European Journal of Forest Research 127, 1-22.

Míchal, I., Petříček, V. (Eds.), 1999. Péče o chráněná území II. Lesní společenstva. Agentura ochrany přírody a krajiny v ČR. Praha (in Czech).

Moravec, J. (Ed.), 1994. Fytocenologie [Phytosociology]. Academia, Praha (in Czech).

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. Biodiversity and Conservation 17, 2979-3001.

Nařízení Vlády České republiky č. 163/1991 Sb., ze dne 20. března 1991, kterým se zřizuje Národní park Šumava a stanoví podmínky jeho ochrany.

Oliver, C.D., 1981. Forest development in North America following major disturbances. Forest Ecology and Management 3, 153–168.

Pouska, V., Lepš, J., Svoboda, M., Lepšová, A., 2011. How do log characteristics influence the occurrence of wood fungi in a mountain spruce forest? Fungal Ecology 4, 201-209.

Romme, W.H., Everham, E.H., Frelich, L.E., Moritz, M.A., Sparks, R.E., 1998. Are large, infrequent disturbances quantitatively different from small, frequent disturbances? Ecosystems 1, 524-534.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., Small, T.W., 1989. Tree uprooting: review of impacts on forest ecology. Vegetatio 79, 165-176.

Schelhaas, M. J., Nabuurs, G. J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology 9, 1620-1633.

Svoboda, M., Pouska, V., 2008. Structure of a Central-European mountain spruce old-growth forest with respect to historical development. Forest Ecology and Management 255, 2177-2188.

Svoboda, M., Janda, P., Nagel, T. A., Fraver, S., Rejzek, J., Bače, R., 2012. Disturbance history of an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. Journal of Vegetation Science 23, 86–97.

Svoboda, M., Fraver, S., Janda, P., Bače, R., Zenáhlíková, J., 2010. Natural development and regeneration of a Central European montane spruce forest. Forest Ecology and Management 260, 707-714.

Svoboda, M., Matějka, K., Kopáček, J., 2006. Biomass and element pools of selected spruce trees in the catchments of Plešné and Čertovo Lakes in the Šumava Mts. Journal of Forest Science 52, 482-495.

Ulanova, N., G., 2000. The effects of windthrow on forest at different spatial scales: a review. Forest Ecology and Management 135, 155-167.

Ulbrichová, I., Remeš, J., Zahradník, D., 2006. Development of the spruce natural regeneration of mountain sites in the Šumava Mts. Journal of Forest Science 52, 446-456.

Vrška, T., Hort, L., Odehnalová, P., Horal, D., Adam, D., 2001. The Boubín virgin forest after 24 years (1972-1996) – development of tree layer. Journal of Forest Science 47, 439-459.

Waring, R.H., Running, S.W., 2007. Forest ecosystems: Analysis at multiple scales, third ed. Academic Press, San Diego, California.

Whitmore, T.C., 1989. Canopy gaps and the two major groups of forest trees. Ecology 70, 536-538.

Zenáhlíková, J., Svoboda, M., Wild, J., 2011. Stav a vývoj přirozené obnovy před a jeden rok po odumření stromového patra v horském smrkovém lese na Trojmezné v Národním parku Šumava [The state and development of natural regeneration before and one year after a dieback in the tree layer of a mountain spruce forest in the Trojmezná area of the Šumava National Park]. Silva Gabreta 17, 37-54 (in Czech, English Summary).

Zielonka, T., 2006. When does dead wood turn into a substrate for spruce replacement? Journal of Vegetation Science 17, 739-746.

Zielonka, T., Piątek, G., 2004. The herb and dwarf shrubs colonization of decaying logs in subalpine forest in the Polish Tatra Mountains. Plant Ecology 172, 63-72.

Żywiec, M., Ledwoń, M., 2008. Spatial and temporal patterns of rowan (*Sorbus aucuparia* L.) regeneration in West Carpathian subalpine spruce forest. Plant Ecology 194, 283-291.

Chapter II: Manuscript draft

Development of Central-European Mountain Spruce Forest 12 Years After Disturbance: Evaluation of Regeneration and Vegetation Changes

(Hrežíková, M., and Edwards-Jonášová, M.)

Abstract

Disturbances are an important factor influencing the dynamics and structure of mountain spruce forests. In the Šumava National Park (the Bohemian Forest) on the southwest border of the Czech Republic, the main disturbance agents are storm events resulting in windthrows and subsequent bark beetle (*Ips typographus* (L.)) outbreaks.

In the 1990's, bark beetle outbreak resulted in the large-scale dieback of semi-natural mountain spruce (*Picea abies* (L.) Karst.) forests in the central part of the national park. Two applied management measures enabled a long-term comparison: 1) core zones left without intervention, and 2) surrounding zones clear-cut – infested trees felled and removed – and cleared areas replanted. Plots were established in acidophilous mountain spruce forests with no intervention and which were developing spontaneously, in the same type of forest but clear-cut with artificial regeneration, and edaphically conditioned waterlogged spruce forests without intervention. Amount and vertical structure of tree regeneration and vegetation changes have been studied on 18 permanent plots (0.04 ha each) since the beginning of the disturbance in 1997.

The main question of the study was if tree regeneration and herb-layer vegetation differed between spontaneously developing disturbed stands and clearcuts after 12 years. Multivariate analyses of vegetation composition and tree regeneration, supplemented by ANOVA of numbers of spruce and rowan, confirmed differences between the applied management methods; there was a more unified height structure of spruce regeneration in the case of clearcut with artificial regeneration. In the spontaneously developing stands, natural regeneration was sufficient to replace the previous canopy and will probably create a more diversified stand. The direct regeneration of previous tree species composition followed the bark beetle outbreak in the spontaneously developing stands. Due to a less harsh change in site conditions and no damage from logging, typical herb species flourished in the non-intervention zones in comparison to the clear-cuts. The impact of post-disturbance interventions on the herb-layer vegetation was significant even twelve years after the event.

Spontaneous recovery of the forest follows natural disturbances and maintains its structural and biological diversity.

Key words: mountain spruce forest, bark beetle outbreak, disturbance, salvage logging, natural regeneration, herb-layer vegetation

1 Introduction

Natural disturbances represent an important part of the mountain spruce forest dynamics (Svoboda et al., 2012). They determine proportions of stands of various stages of development on the landscape level (Frelich, 2002). In the last few years, several studies from Central Europe and especially from the Šumava Mts. dealt with reconstructions of disturbance history to shed more light on the range of historical variability for the forest ecosystems in the region as traditional views considered the large disturbances only as unnatural and happening nowadays due to previous forestry practices (Svoboda et al., 2012). It was revealed, that historical range of variability of these forests comprise continuum from the small-scale gap dynamics to large-scale, high-severity disturbances occurring at various temporal and spatial scales; unlike the previously accepted view that dynamics is driven only by gap dynamics of small cycle with endogenous tree mortality (Brůna et al., 2013; Čada et al., 2013; Svoboda and Pouska, 2008; Svoboda et al., 2010; 2012). In these studies, the historical evidence of natural regeneration of mountain spruce forest ecosystems following large-scale disturbances was proved.

The main disturbance agents occurring in the Šumava Mts. are wind and bark beetle and some of the recent bark beetle outbreaks initiated by strong wind have been recently observed in the bark beetle outbreaks along Germany-Czech border in the Bayerischer Wald (Heurich et al., 2001) and the Šumava Mts. (since 1990s: Jonášová and Prach, 2004), along Slovak-Polish border in the Tatra Mts. (since 2004: Jonášová et al., 2010), or in the Swiss Alps (since 1990s: Kupferschmid and Bugmann, 2005).

When such large-scale disturbances occur, however, there is usually a need to prevent its spreading (Ilisson et al., 2007; Lindenmayer et al., 2008). Traditionally, the disturbed stands were logged with aim to salvage at least the timber and to prevent further progress of the bark beetle outbreak even in the Šumava Mts. with the tendencies to use the same management even in the most protected zones of the Šumava National Park (Čížková, 2010; Zatloukal, 1998). As the result, there has been a general lack of knowledge of regeneration processes after disturbances of the mountain spruce forests in Central Europe as the forests with spontaneous development after the disturbances were very rare (Heurich, 2009; Schelhaas et al., 2003).

The requirement for salvage logging in the protected areas, however, contradicts the conservation objective to enhance forest biodiversity and natural processes (Bässler et al., 2012). Protected landscape areas are the very especial places where the last remnants of more or less natural forests stayed preserved; what is true mainly within highly populated Central Europe. The first origins of no-management in the region of the Šumava Mts. come from the Bayerischer Wald National Park after the strong winds of 1983 and 1984 that caused large-scale windthrows that were decided to be left without any interventions as they were located within the protected area (Heurich et al., 2001). Since that time, the spontaneous development of the forest including the regeneration processes have been studied in windthrows and dead wood stands disturbed by bark beetle on the German side of the border (Fischer et al., 2002; Heurich, 2001; 2009; Jehl, 2001). The role of bark beetle as key-stone species has been recently clarified for the mountain spruce forest (Müller et al., 2008; 2010) and the forests have proved the ability to regenerate without any additional plantings after the natural disturbances (Heurich, 2009). Since the late 1990s, surveys of regeneration processes have come also from the Czech side (Jonášová and Matějková, 2007; Jonášová and Prach, 2004) and recently other studies considering regeneration processes have been conducted (Bače et al., 2009; 2012; Svoboda et al., 2010; Zenáhlíková et al., 2011).

This study recorded more than decade of the earliest phase of the forest development after the disturbance caused by bark beetle outbreak and consequent sanitation felling and salvage logging operations in spruce forests in the central part of the Šumava National Park since the half of 1990s with the following objectives. Firstly, to present the comparison of both spontaneously developing disturbed forest stands and clearcut stands during twelve years of post-disturbance development. Secondly, to outline the spontaneous development of both climatically and edaphically conditioned spruce forests. These aspects together make the study rather rare in the context of Central Europe.

The questions were: 1) Are the differences between spontaneously developing stands and the clearcuts noticeable twelve years after the onset of disturbances? 2) How does tree regeneration evolve through time? 3) How does species composition of the herb-layer vegetation differ or change over time in forests with or without interventions?

2 Methods

2.1 Study Area

The study area was located in the central part of the Šumava Mts. (the Bohemian Forest), on the SW of the Czech Republic (48°56’ – 48°59’ N, 13°25’ – 13°29’ E; 1175 – 1280 m a. s. l.). Since 1991, the area has formed the central part of the Šumava National Park, extending along the border with the Bayerischer Wald (the Bavarian Forest) National Park, Germany.

Quite mild relief represents an extensive undulating plateau called “Šumavské Pláně” with mean altitude about 1000 m a. s. l; which is locally overtopped by rounded mountain ridges above 1200 m a.s.l. with rather gentle slopes (Neuhäuslová, 2001a). Therefore, the nature of the vegetation cover was probably formed mainly by altitude, moisture conditions, and atmospheric circulation rather than by landscape configuration (Neuhäuslová, 2001a). The bedrock is built up of metamorphic migmatite, partly of igneous biotitic granite up to granodiorite (Czech Geological Survey, 2012). Both are acidic and rather poor in accessible nutrients for plants (Neuhäuslová, 2001a). Podzols are prevailing soil group; accompanied by histosols, developed on waterlogged shallow slopes and in depressions where peat was formed, and gleysols on non-calciferous deluviofluvial and fluvial sediments (Neuhäuslová, 2001a). The position on the transitional zone of the Central-European temperate climate brings both the oceanic and continental influences (Neuhäuslová, 2001a). The area has boreal climate with a short, cold, and humid summer; very long transition periods with a cold spring and moderately cold autumn; and a very long, very cold, and humid winter with a long-lasting period of a snow cover (Tolasz et al., 2007). Otherwise, a slightly milder type of the cold climate follows up towards the lower altitudes. Mean annual temperature is about 4 °C and mean annual precipitation about 1500 mm comes usually with the prevailing Western winds (Neuhäuslová, 2001a). The vegetation period is short, only about 150 days (Neuhäuslová, 2001a), what coniferous forests tolerate better than the broad-leaved forests (Moravec et al., 2002).

The study area is characterized by forest complexes of mountain spruce forests (of alliance *Piceion excelsae* Pawłovski in Pawłovski, Sokołowski et Wallish 1928), which formation was induced both climatically (climatically conditioned Norway spruce forests) and edaphically (waterlogged Norway spruce forests) (Neuhäuslová, 2001a). Mainly the latter belong to the most valuable and less directly influenced forests. On the ecological gradient, the waterlogged spruce forests change into naturally sparse forest communities (with shrub-like *Pinus* x *pseudopumilio* or with sparsely distributed stunted Norway spruces) around naturally forest free communities of the raised peat bogs (Sádlo, 2001, Neuhäuslová, 2001a).

The climatically conditioned spruce forests spread in the study area over approximately 1200 m a. s. l. (Neuhäuslová, 2001a). Norway spruce (*Picea abies*) dominates in the tree layer; admixed can be rowan (*Sorbus aucuparia*) and in lower altitudes also European beech (*Fagus sylvatica*) and European fir (*Abies alba*). The shrub layer is developed rarely, comprising regenerating spruce and rowan (Moravec et al., 2002). *Calamagrostis villosa, Avenella flexuosa*, and *Vaccinium myrtillus* dominate in the species-poor herb layer. Other typical species are *Homogyne alpina*, *Trientalis europaea*, *Luzula sylvatica*, *Dryopteris dilatata*, *Oxalis acetosella*, and *Galium saxatile* (Moravec et al., 2002).

The other spruce dominated forests are edaphically conditioned *Bazzania trilobata*-rich waterlogged spruce forests. Because of the permanently waterlogged soil, Norway spruce (*Picea abies*) dominates in the tree layer almost exclusively. Rowan (*Sorbus aucuparia*) and birches (*Betula pubescens*, *B. carpatica*) are only rarely admixed. In comparison with the climatically conditioned spruce forests, the herb layer has a lower cover (about 50 % or less) in favour of the well-developed moss layer. *Vaccinium myrtillus* dominates, while *Avenella flexuosa*, *Vaccinium vitis-idaea*, and *Calamagrostis villosa* are also often common. *Dryopteris dilatata*, *Oxalis acetosella*, *Maianthemum bifolium*, *Trientalis europaea*, *Homogyne alpina*, *Lycopodium annotinum*, and *Soldanella montana* rarely supplements the herb layer (Moravec et al., 2002).

The originally extensive forest stands in the higher parts of the Šumava Mts. stayed relatively untouched till the end of the 18th or the beginning of the 19th centuries (Chábera 1987). For the first time, the highest part of the Šumava Mts. was considerably impacted by colonization culminating between the 18th and 19th century, related to glass-works and forest clearance activity. Preferential selection of beech and fir for glass-works, combined with the negative impacts of forest grazing and exploitation of forest litter, caused spruce to spread beyond its original sites (Beneš, 1995).

Thus there are remnants of original or virgin forests, natural forest, together with more influenced near-natural forests (Pralesy.cz, 2004). The health conditions of these stands were beyond the direct forestry impacts impacted by acidification effects and their resistence decreased in the second half of the 20th century (Šantrůčková et al., 2007). Since 1990s, beginnings of the non-intervention regime originate in the area of interest but also the bark beetle infestation increases. As the bark beetle outbreak spread within the Šumava National Park, the core zone was reduced in its extent and resulted in fragmented zones of nature protection where the stands were supposed to be natural and uninfluenced in 1995 (Zatloukal, 1998).

In 1997, the forestry measures to prevent bark beetle spreading took place next to the non-intervention area and resulted in clearcuts (Jonášová and Prach, 2004) and their replanting in the following years. These were the last official forestry measures in the locality since then. The applied management measures enabled not only a long-term observation of the spontaneous development of the disturbed forests after the bark beetle outbreak; but also the confrontation with the outbreak followed by clearcut and replanting. Context of proportions of managements in the study area were visualized by Hais et al. (2009).

Despite the mentioned impacts on the studied area, these ecosystems exhibit more or less natural character (Jelínek, 1988) and the mosaic of forests and peat bogs is still of high importance within the concept of densely populated Central Europe (Čeřovský et al., 2007). The area of interest was classified as an Important Plant Area (Palmer and Smart, 2001).

2.2 Research plots

Eighteen permanent research plots (0.04 ha each) were established in the area of the interest in 1997 and 1998, at the same time as the bark-beetle attack appeared (detailed description in Jonášová and Prach, 2004). Representative parts of the available mature and relatively homogenous spruce stands were chosen based on the advance of the bark beetle spreading and the contemporary creation of clearings in the part of the area (Jonášová and Prach, 2008). The administration of the national park decided to left without any intervention the fragmented zones of the highest value and to prevent the bark beetle spreading from the locality by removal of infested spruce trees by sanitation or salvage logging operations around. The applied management measures enabled the long-term observation of the spontaneous development of the disturbed forests after the bark beetle outbreak; in the confrontation with the outbreak followed by clearcut and replanting.

Stands of the mountain and waterlogged spruce forests were observed and three types of plots were established. 1) "Dead wood stand" (the plot type "D", eight plots) was climatically conditioned mountain spruce forest without intervention and with spontaneous development where the mean crown canopy cover before the outbreak was about 50 % and decreased to 37 % (the percentage then regarded the total cover of both live or dead canopy; see Appendix III) in 1998, 11 % in 2002, and nearly 2 % in 2009 (0.4 % of canopy cover were live trees on average) as the spruces died off and the needles, branches, bark, and finally the trunks gradually fell down. 2) "Clearcut" ("C", five plots) was the same type of forest but stand where the infested spruces were felled, removed, and the slash milled into wood chips and spread on the ground in 1997. In the following years, the clearings were replanted by spruce and rowan. During the last observation in 2009, one plot had to be excluded because of different management than the other clearcut plots (different species composition of plantings and protection against browsing). 3) "Waterlogged dead wood stand" ("W", five plots) was edaphically conditioned waterlogged spruce forest without intervention where the mature spruces were surviving generally longer than in the climatically conditioned mountain spruce forest. The mean crown canopy cover of spruce stayed about 50 % till 1998. After all, it decreased as well – to 29 % in 2002, and nearly 7 % in 2009 (nearly 3 % of canopy cover were live trees on average).

2.3 Data collection

This study adhered to the survey concept defined by Jonášová and Prach (2004; 2008) and used the data gained earlier. The amount and vertical structure of the tree regeneration and vegetation changes of herb-layer were observed in each plot in 1998, 2002, and 2009. When possible, species and saplings were determined as tree species; only admixed birch (*Betula* sp.) and willow (*Salix* sp.) were recorded as genus because several species (sub-species) occurred in the locality and the determination of juveniles is uncertain. The nomenclature of vascular plants was unified according to Kubát et al. (2002).

The numbers of all regenerating species were recorded in defined height categories: I) < 50 cm; II) 50 – 100 cm; III) 100 – 200 cm; IV) ≥ 200 cm. In 2009, two additional subcategories < 20 cm and 20 – 50 cm were also measured. The plots of dead wood stand were established in the proclaimed non-intervention zones (1st zones) where no trees should have been planted (Čížková et al., 2011). However, few planted spruces appeared in one of the plots of dead wood stand. Since it was only 11.5 % of the total number of trees in the plot, the natural regeneration still dominated and the planted trees were hence ignored. As long as it was possible to differentiate between natural regeneration and planted saplings in clearcuts, only naturally regenerating trees were counted in 1998 and 2002. In 2009, only the total amount of regeneration was determined (both natural and planted trees were included).

The percentage covers of all herb-layer species and the total percentage covers of moss layer "E0", herb layer "E1", and tree layer "E3" (the total cover of live or dead canopy, including standing broken snags) were visually estimated, as well as of the other structures like wood (including lying wood and stumps), litter, and bare soil surface. The tree species within the herb-layer vegetation were analysed in analyses of tree regeneration. The small covers below 1 % got the uniform value 0.5 %; or if the occurrence of plants was really rare, it was 0.02 %.

Evaluations per plot were done in four subplots of 0.01 ha. Tree regeneration numbers were then summarized and percentages were averaged, what served as the output data for the further analyses.

2.4 Data analyses

The height structure and species composition of tree regeneration (numbers of all tree species in height categories) and the herb-layer species composition (percentage covers of herb-layer species) in three plot types were evaluated by several multivariate analyses (Lepš and Šmilauer, 2003) using the Canoco for Windows package and the CanoDraw programme for the creation of the ordination diagrams (Ter Braak and Šmilauer, 2009).

Square-root transformations of the numbers and percentage covers were performed to gain the normality. The length of the gradient from Detrended Correspondence Analysis (DCA) was quite short (2.1) in the case of the numbers of tree regeneration, so a linear model was used – Principal Component Analysis (PCA). The unimodal model was chosen (DCA) for herb-layer vegetation as the gradient was longer (3.4). The downweighting of rare herb-layer species prevented their over-emphasized influence.

Interactions among the plot types and years were passively projected into the ordination diagrams, together with other passive variables (total covers of moss, herb, and tree layer, wood, and litter). The years (1998, 2002, and 2009) and plot types (dead wood stand "D", clearcut "C", and waterlogged dead wood stand "W") were used as categories. The influence of the altitude was ignored as the range was only 105 m and its expected effect was minimal.

Constrained analyses, linear Redundancy Analyses (RDA) or unimodal Canonical Correspondence Analyses (CCA), were used to test the relationships between tree regeneration or herb-layer vegetation, respectively, and explanatory variables (the type of the plot and time). Several partial constrained analyses revealed the percent variability in the response data explainable by a particular explanatory variable (whereas the influence of the other variables was eliminated by using them as covariates). In the first analysis (RDA/CCA I), the effect of the plot type (D, C, W) was tested, while time was used as the covariate. The same analysis but only for dead wood stand and clearcut (D and C), tested the effect of the logging operations and the consequent replanting in clearcut on tree regeneration and herb-layer vegetation (RDA/CCA II). The time progress independent of plot type was tested by using years (1998, 2002, 2009) as the explanatory variables and the plot identifiers (1 – 17, coded as dummy variables) as covariates (RDA/CCA III). Further, the interaction of the plot type and time was of the great interest (RDA/CCA IV), especially the comparisons between dead wood stand and clearcut (RDA/CCA V) as they represented the similar conditions in the beginning of the study. Hence, the differences between them corresponded to the management interventions. The interaction tested the null hypothesis that the temporal trend (of tree regeneration/herb-layer vegetation) was independent of plot type (the average over years was subtracted and the changes in the particular plot types only were analysed while plot identifiers and time were the covariates). Finally, to compare the herb species composition twelve years after the disturbance events, differences in herb-layer vegetation among plot types were tested by separate analyses when only data from 2009 season were applied (CCA VI-2009 for D, C, W; CCA VII-2009 for D, C). The statistical significances were tested by the Monte Carlo permutation tests. Analyses III – V used split-plot design (the records done in the same permanent plot were "subplots" of "the main plot" and only "the main plots" were permuted).

Moreover, the differences in total numbers of regenerating spruce and rowan between all pairs of the plot types in particular years were tested by Analysis of Variance (ANOVA) using Statistica 7.0 for Windows programme. Because a clearcut plot for 2009 had to be excluded prior to the analysis, ANOVA with repeated measurements had to be substituted by univariate ANOVA for each separate year. Similarly, to compare the height structure of spruce twelve years after the disturbance events, differences in numbers of seedlings or saplings of each height category (< 20 cm; 20 – 50 cm; 50 – 100 cm; 100 – 200 cm; ≥ 200 cm) among plot types were tested by separate univariate ANOVA for data from 2009. The data were square-root transformed beforehand to meet the assumption of the analysis. Homogeneity of variances was tested by Hartley-Cochran-Bartlett test.

3 Results

3.1 Tree regeneration

Altogether six tree species were found on the research plots during the observations: Norway spruce (*Picea abies*), rowan (*Sorbus aucuparia*), birch (*Betula* sp.), willow (*Salix* sp.), aspen (*Populus tremula*), and European beech (*Fagus sylvatica*) (numbers of regenerating tree species for each plot type in 1998, 2002, and 2009 presented in Appendix I). With spruce dominating and rowan forming an admixture, the tree regeneration reflected the previous tree layer species present after the disturbance in all plot types. Considering the total numbers of regenerating spruce and rowan, the variability among the plot types was obvious (Fig. 3, Appendix I) but less significant in separate analyses for each year (Tab. 2).

Total numbers of spruce regeneration almost significantly differed between the dead wood stand and clearcut in 1998 (Tab. 2). In dead wood stand, the total numbers of spruce decreased during the years after the dieback, yet stayed the highest in comparison with the other plot types. In 1998, the lowest numbers of spruce as the advanced regeneration that survived the logging operations were found in clearcut and the numbers further decreased till 2002. The inclusion of artificial regeneration in 2009 balanced the numbers of spruce in clearcut with the level of natural spruce regeneration in dead wood stand. After the previous decrease till 2002, a natural supply of new spruce seedlings increased the total spruce numbers also in waterlogged dead wood stand between 2002 and 2009. Hence, the total numbers of spruce did not differ between clearcut and both spontaneously developing types of plot in 2009 in spite of afforestation (Tab. 2, Fig. 3a) and even slightly more trees were present in dead wood stand than in clearcut after replanting (see Appendix I).

Total numbers of rowan were much lower (several individuals per 0.04 ha plot, see Appendix I). The highest numbers of rowan were observed in dead wood stand in 2002 (significantly higher than in waterlogged dead wood stand and almost significantly higher than in clearcut; Tab. 2, Fig. 3b). After this increase of rowan in dead wood stand, its numbers again decreased till 2009 but remained approximately twice higher than in 1998. In clearcut, the numbers of rowan increased each year of observation and it slightly exceeded the numbers of rowan in dead wood stand in 2009 (due to the replanting). The plots of waterlogged dead wood stand were quite poor in rowan in 1998, but the rowan appeared more frequently in these plots later, although it stayed lower than in the plot types of climatically conditioned spruce forest.

Other tree species reached generally very low numbers (therefore not tested) and their presence related with particular plot types (see Appendix I). Beech seedlings appeared as rare exemplars in dead wood stand shortly after the disturbance and also in waterlogged dead wood stand in 2002; none of them was observed in 2009, though. In clearcut, the numbers of commonly regenerating spruce and rowan were generally lower in 1998 but the tree composition was enriched by pioneer species such as birch, willow, and aspen which persisted till 2009. Birch became a typical admixture in clearcut plots and increased its frequency each year. In 2002, birch and rarely willow appeared also in some plots of waterlogged dead wood stand, while birch reached high numbers in 2009, willow was not observed again.

In addition to the total numbers of the trees, the height structure of the observed trees offered further information on the regeneration. For instance, it showed also height increments of spruces during the time and indicated poor supply of the youngest spruces in clearcut during the observation period in comparison with the spruce forest stands without any intervention (see Fig. 4). In the PCA ordination diagram (the first ordination axis explained 79.6 % and the second axis 10.3 % of variability, Fig. 1); the passively projected centroids of each plot type changed their positions within the ordination space during the time (Fig. 1b) according to numbers of regenerating tree species in particular height categories (Fig. 1a).

Shortly after the disturbance (or before for some individual plots of waterlogged dead wood stand) in 1998, the high numbers of spruce seedlings bellow 50 cm characterized dead wood stand and waterlogged dead wood stand, while this category was much lower in clearcut. Nonetheless, the dead wood stand and the clearcut showed noticeable time progress with the similar tendencies since 2002, what related mainly with the increasing numbers of trees in the higher categories, especially spruce and rowan above 100 cm. Instead, the plots of waterlogged dead wood stand were less homogenous considering the tree regeneration and generally showed rather different development with lower numbers of spruce in higher categories (mainly above 100 cm), lower numbers of rowan in comparison with the climatically conditioned forest stands, and the presence of birch in some individual plots.

As a consequence, the RDA analyses (Tab. 1) tested the general time progress in the height structure and species composition of tree regeneration independent of plot type and explained much more variability (RDA III) than also significant differences among the three plot types (RDA I). As this time progress related to some extent to growth of seedlings and saplings, the differences among the individual temporal developments of plot types (interaction of plot type and time) were found closely not significant (RDA IV), so were the individual temporal trends between only dead wood stand and clearcut (RDA V). Nevertheless, significant differences in height structure of regenerating tree species were confirmed for dead wood stand and clearcut (RDA II), what tested the effect of the logging operations and the consequent replanting in clearcut on tree regeneration.

Besides, the numbers of spruce regeneration were tested separately for 2009 (Tab. 3) since more detailed height categories (< 20 cm, 20 – 50 cm, 50 – 100 cm, 100 – 200 cm, ≥ 200 cm; Fig. 5) illustrated the supply of the youngest spruces. Several univariate ANOVAs revealed variations in height structure between the plots. While numbers of trees in middle height categories (20 – 50 cm, 50 – 100 cm) did not result in significant differences, dead wood stand and clearcut significantly differed in the amount of the smallest seedlings and saplings (< 20 cm) in favour of dead wood stand. On the other hand, clearcut had significantly more of the highest spruces (≥ 200 cm) compared to both dead wood stand and waterlogged dead wood stand. Waterlogged dead wood stand was generally poorer in higher spruces than the climatically conditioned spruce forests (100 – 200 cm). Consequently, the significantly different height structure indicated differences in the future development of the plots with and without the management operations as the main role play the youngest tree seedlings which were almost absent in the clearcut.

3.2 Herb-layer vegetation

The DCA ordination diagram showed the relations among herb-layer species within the ordination space (Fig. 2a) where the first ordination axis explained 31.3 % and the second axis 12.0 % of variability. The centroids of each plot type in the particular year, displayed within the same ordination space as for the species, showed positions of climatically and edaphically conditioned spruce forests along the first axis (Fig. 2b) based on their species composition. Dead wood stand (bottom left) and clearcut (upper left) were clearly separated from waterlogged dead wood stand (right).

In the climatically conditioned spruce forest, grasses *Calamagrostis villosa* and *Avenella flexuosa* dominated the herb-layer. After an increase of their cover in 2002, both of them were observed on the level of almost 30 % in clearcut in 2009. In dead wood stand, *Calamagrostis villosa* held its increased level from 2002 (almost 40 %) and *Avenella flexuosa* its decreased level from 2002 (about 15 %). While *Luzula sylvatica* was third dominant species and slightly increased during the years in clearcut, it was less abundant in dead wood stand and even decreased till 2009. On the contrary, third most abundant species of dead wood stand was *Vaccinium myrtillus* which, in spite of a decrease in between 1998 and 2002, held its level till 2009, whereas it reached much lower abundances in clearcut, despite its increasing tendency. *Galium saxatile* seemed to be a species favouring from the disturbance as it increased its low abundance. Pioneer and light-demanding species *Epilobium angustifolium* and *Rubus idaeus* slightly increased within the plots but abundances kept low. Higher abundances were observed in clearcut shortly after the disturbance in 1998 and in 2002. In 2009, *Rubus idaeus* decreased in clearcut to a level comparable with dead wood stand and *Epilobium angustifolium* even increased its abundances in the stands without any intervention over the clearcut levels, what occurred both in dead wood stand and waterlogged dead wood stand. *Taraxacum* sect. *Ruderalia*, plant relating with human activity, frequently observed in clearcut since 1998, decreased till 2002 and was even absent in 2009. In contrast, species of wet forest openings, like *Juncus filiformis*, *Juncus effusus*, *Luzula campestris* agg. (cf. *sudetica*), *Carex ovalis*, were rarely observed in clearcuts in 2009. On the other hand, ferns *Athyrium distentifolium* and *Dryopteris dilatata* and herbs *Trientalis europaea, Homogyne alpina, Soldanella montana,* and *Oxalis acetosella* frequently occurred in dead wood stand in low abundances, but only exceptionally or with lower abundances in clearcut. *Lycopodium annotinum* increased rare abundances in dead wood stand and waterlogged dead wood stand, whereas it even decreased the rare presence in clearcut.

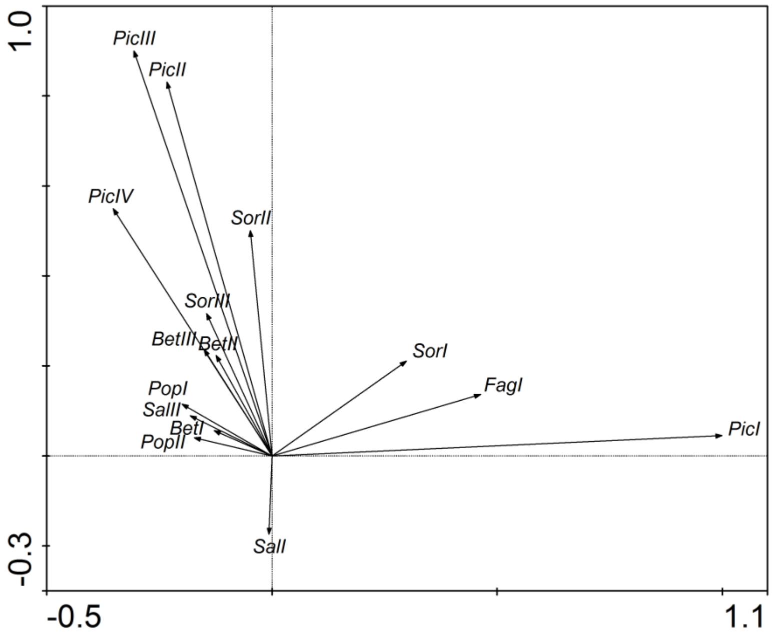
The waterlogged spruce forest differed in species composition from the beginning, however it underwent a gradual change with more or less similar tendency since 1998, which appeared as nearing to climatically conditioned spruce forest. Dominating *Vaccinium* *myrtillus* slightly increased its high abundance to about 30 % and *Vaccinium vitis-idea* slightly increased its rare abundance, though. Quite abundant species *Eriophorum vaginatum* decreased till 2009 by half and other moisture demanding species *Molinia caerulea*, *Carex echinata* or other *Carex* species (*C. nigra* or *C. rostrata*) slightly decreased their covers as well. In contrast, grasses *Calamagrostis villosa* and *Avenella flexuosa* slightly increased their low abundances and *Epilobium angustifolium*, *Rubus idaeus*, *Galium saxatile* and *Deschampsia cespitosa* were firstly observed with increasing tendency in 2002 and *Luzula sylvatica* in 2009. Moreover, species typical for climatically conditioned spruce forest *Dryopteris dilatata*, *Trientalis europaea*, and *Lycopodium annotinum* increased in between 1998 and 2009 and *Athyrium distentifolium* was firstly observed in rare abundances in 2009. Nevertheless, rare exemplars of *Dryopteris cambrensis* and *Carex pauciflora* were observed only in waterlogged type of spruce forest for the first time in 2009.

The CCA analyses (Tab. 1) revealed that the plot type explained the highest amount of variability in the herb-layer species data (CCA I). Further, the community experienced significant changes after the disturbance, although the time progress independent of the plot type accounted for less amount of variability (CCA III). When this general change was filtered out, the interaction of the plot type and time showed significantly different developmental trends of herb-layer vegetation among all tree plot types (CCA IV).

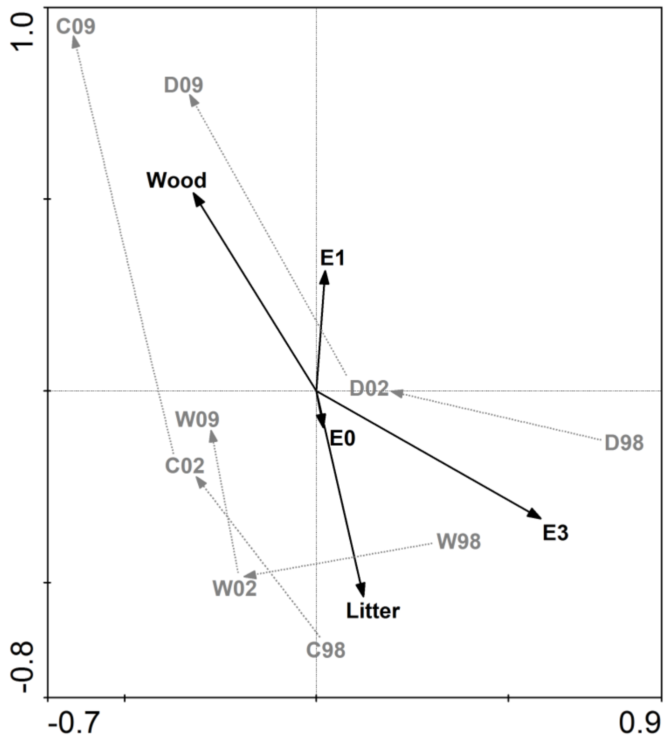
The significant effect of the plot type on the herb-layer species composition and abundances was confirmed not only for all three plot types together but also for comparison of forest stands differing in management interventions. Although it appeared from the positions of plot centroids (Fig. 2b) that herb-layer vegetation of dead wood stand and clearcut in particular years was quite similar, they differed significantly (CCA II). Consequently, the developmental trends of herb-layer vegetation between them also varied (CCA V). The analyses and the ordination diagram (Fig. 2b) indicated that the differences in herb-layer vegetation caused by logging operations deepened till about 2002 (5 years after the operations). In 2009 (12 years after), dead wood stand and clearcut got closer each other but significant differences lasted between them (CCA VII-2009). It supported the assumptions that logging operations had negative effect on the herb-layer vegetation, which was apparent even twelve years after the disturbance.

Tab. 1. ***Results of the multivariate analyses: RDA for tree regeneration and CCA for herb-layer vegetation.*** *The explained variability meant the variability explained by particular explanatory variables (the plot types: dead wood stand – D, clearcut – C, waterlogged dead wood stand – W; years: 1998, 2002, 2009) out of the total variability in the data of tree regeneration or herb-layer vegetation (of all years or of only 2009 data), while the variability of the covariates (Year; Plot ID – identifier of each plot) was subtracted. "*" indicated the interaction between the variables. F-ratio statistics for the test on the trace – F and corresponding probability value – p, obtained by the Monte Carlo permutation test (999 permutations), represented the results of testing the hypothesis that there was no effect of the explanatory variables.*

Analysis	Explanatory variables	Covariates	Explained variability (%)	F	p
Tree regeneration					
RDA I	Plot type (D-C-W)	Year	10.2	2.72	0.0060
RDA II	Plot type (D-C)	Year	9.9	3.74	0.0120
RDA III	Year	Plot ID	31.6	23.77	0.0010
RDA IV	Plot type (D-C-W) * year	Plot ID, Year	5.2	2.26	0.0588
RDA V	Plot type (D-C) * year	Plot ID, Year	3.8	2.53	0.0940
Herb-layer vegetation					
CCA I	Plot type (D-C-W)	Year	33.0	12.43	0.0010
CCA II	Plot type (D-C)	Year	14.8	6.29	0.0010
CCA III	Year	Plot ID	3.4	2.98	0.0010
CCA IV	Plot type (D-C-W) * year	Plot ID, Year	4.9	2.62	0.0010
CCA V	Plot type (D-C) * year	Plot ID, Year	5.0	2.85	0.0010
CCA VI-2009	Plot type (D-C-W)	-	34.2	3.64	0.0010
CCA VII-2009	Plot type (D-C)	-	19.3	2.39	0.0050

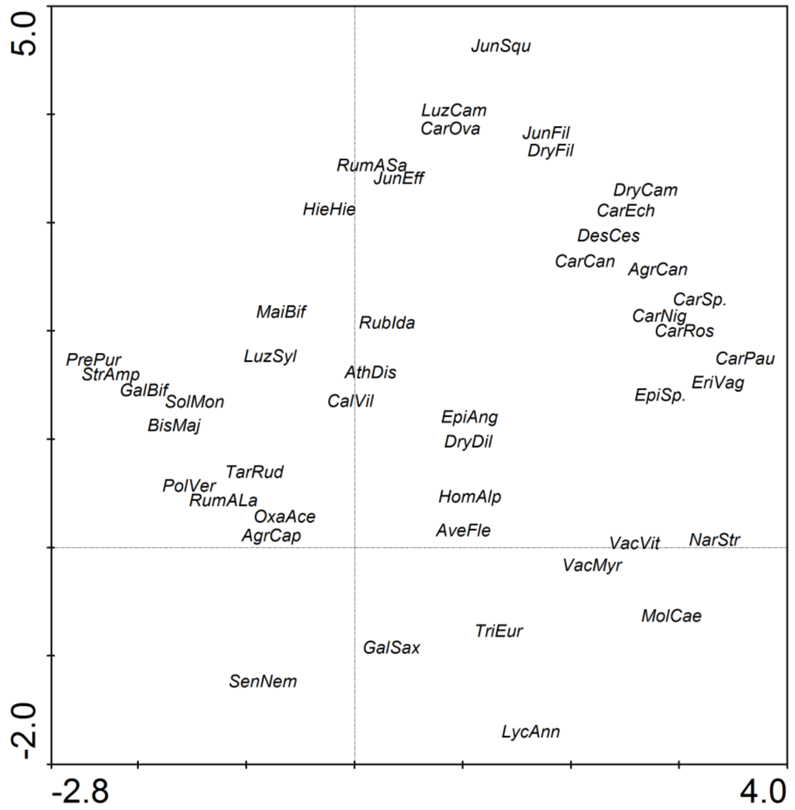


(a)

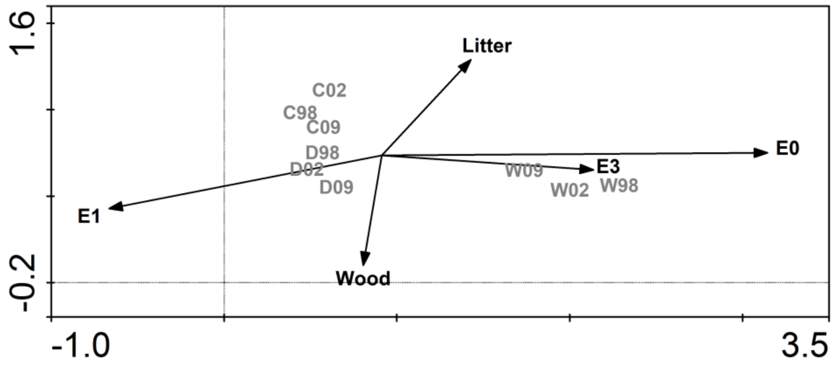


(b)

Fig. 1 a, b. PCA ordination projections of (a) ***numbers of tree species regeneration*** *(the species were labelled by the first three letters of the latin genus; full name and numbers of all species in particular years – viz. Appendix I.) in height categories (I) < 50 cm, II) 50-100 cm, III) 100-200 cm, IV) > 200 cm) and (b)* ***passively projected explanatory variables*** *(centroids of the plot types: dead wood stand – D, clearcut – C, waterlogged dead wood stand – W; in particular years 1998, 2002, 2009; the light arrows indicated the directions of the move)* ***and other characteristics of plots*** *(total covers of: moss-layer vegetation – E0, herb-layer vegetation – E1, live or dead tree canopy, including snags – E3; litter, and wood – including logs and stumps). 1. ordination axis explained 79.6 %, 2. axis 10.3%.*



(a)

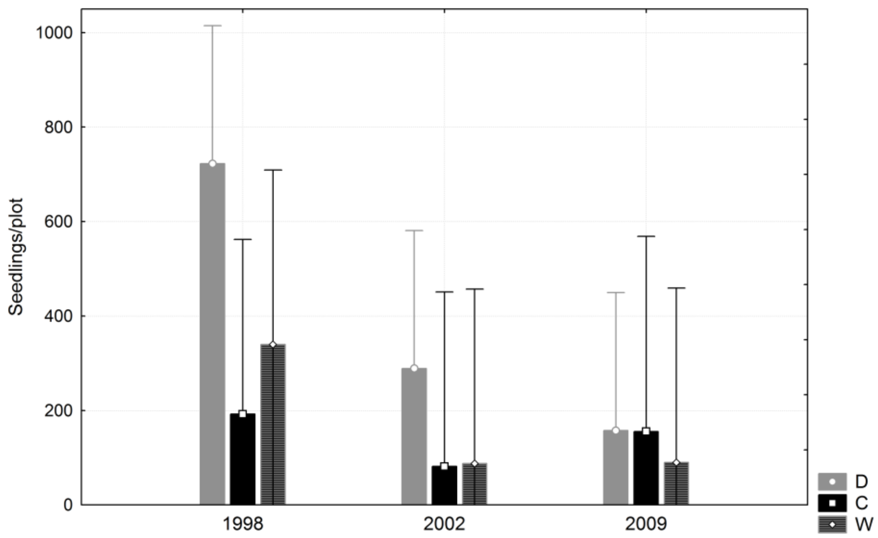


(b)

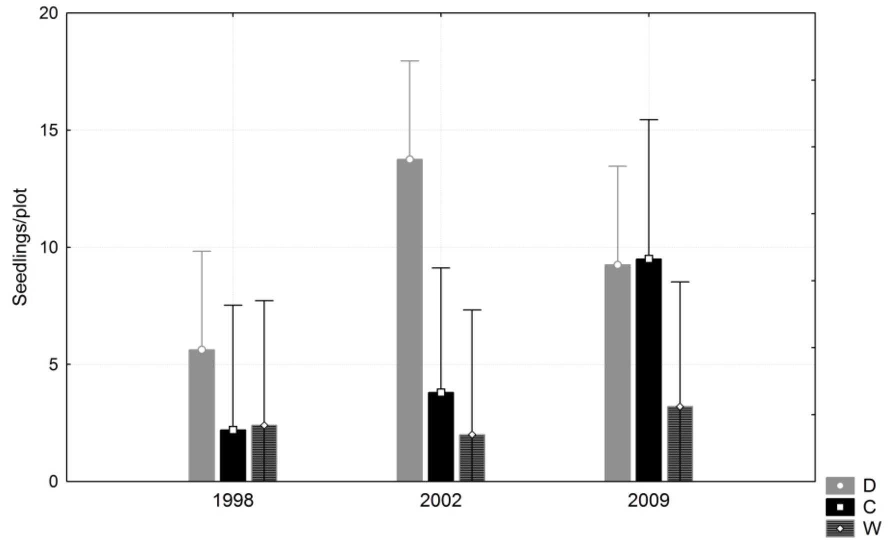
Fig. 2 a, b. DCA ordination projection of (a) ***covers of herb-layer species*** *(the species were labelled by the first three letters of the latin genus and of the species name; full list of species – viz. Appendix II.) and (b)* ***passively projected explanatory variables*** *(centroids of the plot types: dead wood stand – D, clearcut – C, waterlogged dead wood stand – W; in particular years 1998, 2002, 2009)* ***and other characteristics of plots*** *(total covers of: moss-layer vegetation – E0, herb-layer vegetation – E1, live or dead tree canopy, including snags – E3; litter, and wood – including logs and stumps). 1. ordination axis explained 31.3 %, 2. axis 12.0 %.*

Tab. 2. ***Results of the analyses of variance ANOVA for total numbers of the most common tree species – spruce and rowan.*** *The differences among the plot types (dead wood stand – D, clearcut – C, waterlogged dead wood stand – W) were tested separately in particular years. F-ratio statistics – F and corresponding probability value – p represented the results of testing the hypothesis that there was no difference in the numbers of trees among the plot types. Significant differences between pairs of plots, obtained by post hoc Unequal N HSD test, were presented: ** $p \leq 0.01$. The p-values of almost significantly different pairs were 0.054[1] and 0.059[2].*

Analysis	***Spruce***			***Rowan***		
Univariate ANOVA	F	p	Plot differences	F	p	Plot differences
1998	3.26	0.06	D x C [1]	0.99	0.39	
2002	2.25	0.14		8.70	0.0031	D x C [2], D x W**
2009	1.50	0.26		1.48	0.26	



(a)



(b)

Fig. 3. ***Mean total numbers of*** *(a)* ***spruce*** *and (b)* ***rowan regeneration*** *per different types of plot: dead wood stand – D (8 plots), clearcut – C (5 plots till 2002 and 4 plots in 2009), waterlogged dead wood stand – W (5 plots); and in particular years (1998, 2002, 2009). The plot type clearcut in 2009 included planted trees. Column represented the mean number; the whiskers showed the 95% confidence interval.*

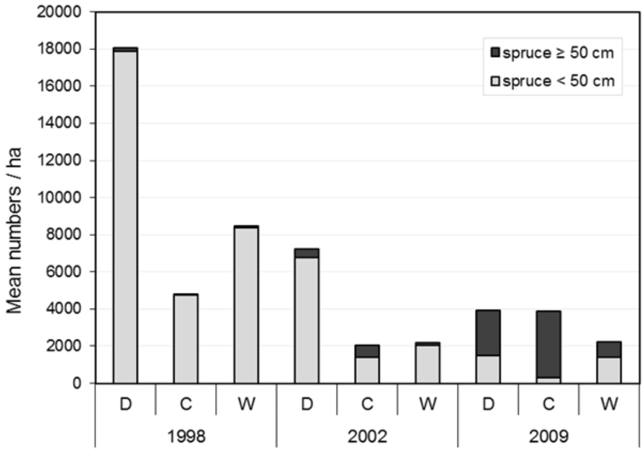


Fig. 4. ***Mean numbers of <u>spruce</u> regeneration in 2 height categories*** *per hectare in different types of plot: dead wood stand – D (8 plots), clearcut – C (5 plots till 2002 and 4 plots in 2009), waterlogged dead wood stand – W (5 plots) and in particular years (1998, 2002, 2009). The plot type clearcut in 2009 included planted trees.*

Tab. 3. ***Results of the analyses of variance ANOVA for numbers of spruce regeneration in height categories.*** *The differences among the plot types (dead wood stand – D, clearcut – C, waterlogged dead wood stand – W) were tested in 2009. F-ratio statistics – F and corresponding probability value – p represented the results of testing the hypothesis that there was no difference in the numbers of trees among the plot types. Significant differences between pairs of plots, obtained by post hoc Unequal N HSD test, were presented: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.*

Analysis	***Spruce in 2009 – height categories***		
Univariate ANOVA	F	p	Plot differences
<20	8.79	0.0034	D x C*
20-50	1.99	0.17	
50-100	2.98	0.083	
100-200	11.06	0.0013	D x W*, C x W*
>200	16.86	0.00018	D x C**, C x W***

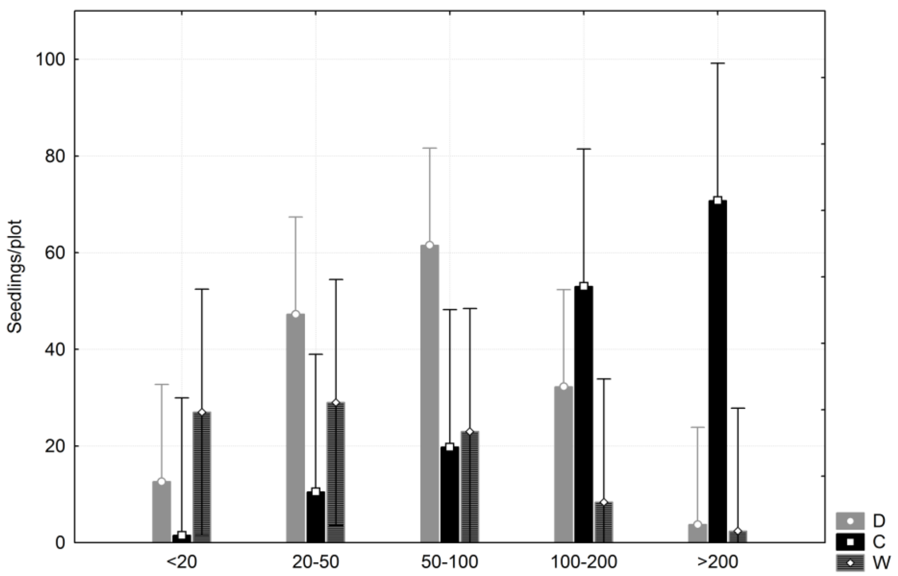


Fig. 5. ***Mean numbers of <u>spruce</u> regeneration in height categories*** *per different types of plot: dead wood stand – D (8 plots), clearcut – C (4 plots), waterlogged dead wood stand – W (5 plots);* ***in 2009****. The plot type clearcut included planted trees. Column represented the mean number; the whiskers showed the 95% confidence interval.*

4 Discussion

4.1 Tree regeneration

Considering the general trends in data, the main change related to growth, what practically resulted in shifts to the higher categories of regeneration. This common pattern for all three plots consequently outweighed the differences in species composition in the multivariate RDA analyses (Tab. 1). Nevertheless, when the growth pattern was not considered, the plot types generally differed in tree species composition among all three plot types as well as among the dead wood stand and clearcut. The latter was the result of post-disturbance loggings (although it explained less of the variability in data). The most dominant species of tree regeneration in all the plot types during the whole twelve years after the post-disturbance development was spruce; rowan formed its admixture; whereas occurrence of other species depended upon the plot type.

In spontaneously developing stands, spruce seedlings and saplings were present as advance regeneration under the previous canopy of mature spruces; and since the outbreak they naturally decreased as the supply of spruce seeds was limited. The presence and importance of advance regeneration have been already observed in the region (e.g., Bače et al., 2012; Čížková et al., 2011; Jonášová and Matějková, 2007; Jonášová and Prach, 2004; Svoboda et al., 2010; Zenáhlíková et al., 2011).

In both spontaneously developing stands, the category below 50 cm represented the highest portion of regeneration (hundreds per plot < 50 cm; see Appendix I; Fig. 4) but the numbers were lower in waterlogged stand when compared to dead wood stand. Whereas this category consisted of both the youngest seedlings (below 5 years) and the older ones in dead wood stand, the older seedlings and saplings were rare in waterlogged stand (observed by Jonášová and Prach, 2004). Moreover, the saplings above 50 cm were rare in both stands (several individuals per plot) in 1998. The reason for lower numbers of older seedlings could be result of unfavourable light conditions under dense canopy (Jonášová and Prach, 2004; Zenáhlíková et al., 2011) or the effect of dead wood removal in the past (as Svoboda and Pouska (2008) observed more diverse density and height of spruce on plots with minor logging activity in the southern part of the Šumava National Park). As for the former, although spruce is able to tolerate shade for some time, individuals die and are replaced by other ones if the light conditions are insufficient for longer time (Bače et al., 2009; 2012; Svoboda et al., 2010; Zielonka, 2006), what could be the case especially of waterlogged spruce stands. The youngest seedlings could be the outcome of the mast year in 1995 (Jonášová and Prach, 2004), two years prior the die-back majority of spruce trees in dead wood stands and three or four (and even fourteen in the case of one plot) years prior the die-back in the waterlogged stands (see decrease in tree canopy in Appendix III). Also in the Bayericher Wald National Park, Heurich (2009) observed increased numbers of spruce regeneration after the mast years and detected the coincidence of bark beetle outbreak and increased production of cones and seeds by spruce. Consequently, the spruce stands ensure the abundant supply of seeds prior to their decay (Heurich, 2009; Kupferschmid et al., 2006 – in Swiss Alps). Nevertheless, they can again decrease if the opening of canopy is delayed (Heurich, 2009). Possibly, the lower numbers in waterlogged stands could be the result of both the factors that relate to the specific conditions in waterlogged dead wood stands which proved to resist the bark beetle outbreak for longer time (see Appendix III for the percentage level of surviving canopy in 2009).

The twelve years of development in the spontaneously developing stands were represented mainly by the decrease in total numbers of spruce (Fig. 3a) as the small seedlings in the lowest category are most susceptible to mortality according to findings of Zenáhlíková et al. (2011). They observed in the region (southern part of the Šumava Mts.) that numbers of spruce discontinue decreasing after they reached at least 4 years and 10 cm. Thus, lower decrease for older and higher saplings is expected in next development of dead wood stand. In waterlogged dead wood stand, the decrease may continue. Nevertheless, the lower abundance of regeneration in waterlogged dead wood stands should not been viewed as a disadvantage but rather as a prerequisite for more heterogeneous landscape structure in the locality. On the other hand, the saplings grew during the twelve years, so that spruces lower than 20 cm occurred, as well as some of height above 200 cm (Fig. 5).

From other species, mainly rowan occurred in spontaneously developing stands. It increased its total numbers under dead wood stand up to the fifth year (2002) after the dieback (Fig. 3b) because this species is also favoured by increased light conditions (Motta, 2003). The fact that the increase did not continue till 2009 could be explained by the mechanism of its dispersal as it seems to depend on foraging behaviour of birds that defecate its seeds when they perch on the large trees (Żywiec and Ledwoń, 2008). Other explanation could be effect of browsing, which was obvious by majority of rowan saplings in 2009. Falling dead branches acted as good protection against browsing in several first years after dieback of tree layer. Beech (and willow in waterlogged dead wood stand) was not observed again in 2009; they were of very low numbers to draw some conclusion from it, though (Appendix I). Nevertheless, birch was observed in waterlogged dead wood stand since 2000 (Jonášová and Prach, 2004) due to the old seed tree nearby that supplied the plot with extraordinary high numbers of individuals (compare mean and median numbers in Appendix I). Nonetheless, it has effect probably more on the local increase in tree diversity than that would it play any crucial role in the composition of waterlogged spruce forests.

In conclusion, the observed total numbers of natural regeneration in spontaneously developing stands are in consistency with the large-scale inventories provided in the Šumava National Park (Čížková et al., 2011) and the Bayericher Wald National Park (Heurich, 2001; 2009). After the twelve years after bark beetle outbreak, we can confirm the ability of spontaneously developing stands to regenerate and to regenerate directly the pre-disturbance tree species composition. No change to initial forest of pioneer species after the large-scale disturbance have been indicated since the beginning of this long-term observation (Jonášová and Prach, 2004), similarly as of the observations by Heurich (2009) or other studies. Čada et al. (2013) demonstrated high plasticity and tolerance of spruce to different light conditions and suggested that spruce can sustain the period of slow growth in lower parts of the canopy and again accelerate its growth at older ages.

In contrast to the spontaneously developing stands, the tree regeneration was significantly affected by post-disturbance logging in clearcut. Firstly, the height structure of advance regeneration of pre-disturbance stand was simplified (Jonášová and Prach, 2004). The lowest category of spruce seedlings was eliminated in clearcut in comparison to spontaneously developing dead wood stand (almost significantly lower numbers of spruce in 1998; Tab. 2, Fig. 3a); probably due to mechanical damage by machinery during the logging; and due to suddenly changed microclimatic conditions (Foster and Orwig, 2006; Jonášová and Prach, 2004; Lindenmayer et al., 2008). Out of the category below 50 cm, the dual disturbance affected mainly the youngest seedlings (Jonášová and Prach, 2004), while a proportion of older seedlings survived. Jonášová et al. (2010) observed saplings older than 10 years even in a cleared windthrow in the Tatra Mts. where these saplings did not significantly differed among plots with or without the intervention.

Secondly, the additional disturbance also increased the germination of pioneer species on the disturbed soil surface (Jonášová and Prach, 2004). They continued to increase up to 2002, while the spruce continued to decrease. Therefore, the proportional change of species composition in clearcut in favour of pioneer species (birch, willow, and poplar) was observed (Appendix I). Increases of these species were observed also elsewhere when soil disturbance occurred in the same locality in similar clearcuts (Jonášová and Matějková, 2007) and in the Bayericher Wald National Park in post-windthrow clearings (Fischer et al., 2002).

However, the final recorded stand structure and composition were affected by artificial regeneration of spruce and rowan that was responsible for increased numbers of spruce and rowan in 2009 (in that year it was included into numbers of regeneration because it could not be clearly distinguished). As the result, the total numbers (mean and median) of spruce and rowan were surprisingly almost identical in 2009 (Appendix I); what means that without the forestry interventions, natural processes are able to ensure the comparable amounts (as also Čížková et al. (2011) concluded). Moreover, the height structure in clearcut was dominated by the young spruces above 200 cm; while the spontaneously developing stands had majority of its regeneration in lower categories (Fig. 5). Not only because of the height of plantings, but probably also because the spruces under fully open canopy of clearcuts resulted in higher increases of terminal leader (Bače et al., 2009). Nevertheless, because the canopy opened due to the outbreak was found to be favourable phase for increase of biodiversity of insect communities, Müller et al. (2008) suggested lengthening it by avoidance of replantings in the mountain spruce forest ecosystem of the region.

Accordingly, the spontaneously developing forests possess properties that could favour the heterogeneity at the landscape-scale (climatically conditioned versus delayed waterlogged forests) and also at the stand-scale as there is significantly more seedlings bellow 20 cm than in clearcut in 2009. However, we cannot deduce that the individuals within the category germinated after the disturbance as right in this height they could be fourteen years old (as tested Zenáhlíková et al., 2011). Nevertheless, some new supply was observed in the first five years of the observation by (Jonášová and Prach, 2004). There were found mature spruce individuals (and rowans) that survived the outbreak and they also continued to produce seeds and were usually responsible for the outstanding observed total numbers in some particular parts of the forest (pers. obs.). This confirms the ability of some individual spruces to survive the bark-beetle attack and to serve as a well-adapted source of seeds. The influx of seeds from the survived trees supplements the biological legacy of the disturbance – in the form of tree regeneration – with the potentially resistant spruce individuals. The survivorship was for the locality assessed to 1-5 % (Jonášová and Prach, 2004) and similarly in the Swiss Alps to about 2 % (Kupferschmid and Bugmann, 2005). As the result, the more opened canopy in spontaneously developing stands may enable the successful establishment of these genetically well-equipped spruce individuals in the future to increase the variability and heterogeneity of stand structure of these forests (Kuuluvainen, 2002). In addition, Heurich (2001) calculated that although only individual or small clumps of old spruces survived, their seeds could reach 66 % of the study area in the Bayerischer Wald National Park (Heurich, 2001). When the characteristics of resistant trees were studied, spruces with a higher level of stem shading (longer crown length) tended to survive (Jakuš et al., 2011). In contrast, clearcut management prevented survival of resistant spruces when it preventively removed all the spruces from the disturbed forests; what has the long-term genetic consequences (Lindenmayer et al., 2008).

4.2 Herb-layer vegetation

Unlike the tree species, the three types of plots explained the most of variability in the data of herb-layer vegetation; especially the climatically and edaphically conditioned spruce forest stands differed (multivariate CCA analyses, Tab. 1). Consequently, the temporal trends of each plot type were also significant. As the result, the significant differences among three plot types; and also between dead wood stand and clearcut proved the significant effect of post-disturbance intervention after twelve years.

The climatically and edaphically conditioned forest stands were well distinguished by specific species composition, despite the species that occurred mainly in relation to the disturbance. Wild et al. (2004) explained the differences by moisture gradient. In the climatically determined forest stands, most abundant species were grasses, *Avenella flexuosa*, and *Calamagrostis villosa*, in both dead wood stand and clearcut. In clearcut, these grasses were observed in particularly high abundances in 2002 (Jonášová and Prach, 2008). Since then, their covers decreased but they continue to dominate the herb layer in clearcuts. The third most abundant and increasing species in clearcut was *Luzula sylvatica* whereas it decreased till 2009 in dead wood stand. On the other hand, the conditions of clearcut were not probably favouring *Vaccinium myrthillus* as it much decreased in clearcuts in comparison to spontaneously developing stands.

The clearcuts differed from the spontaneously developing dead wood stands since the beginning (direct and indirect consequences of logging operations as discussed for seedlings). In relation to effect of loggings on the soil surface, the colonization of some species was enhanced (Jonášová and Matějková, 2007; Jonášová and Prach, 2008). A high increase in *Rubus idaeus* in clearcuts was probably caused by both disturbed soil surface where seeds well germinated from the soil seed bank and by increased light conditions (Fischer et al., 2002; Mayer et al., 2004). Mayer et al. (2004) tested the colonization of disturbed soil in field experiment in and around the Bayericher Wald National Park and after the *R. idaeus*, also species of the genus *Carex,* including *C. canescens*, *C. echinata*, or *C. ovalis*, and, e.g., *Rumex acetosella* colonized the disturbed surface. These species were also observed in clearcut in this study, similarly as *Epilobium angustifolium, Juncus effusus*, or *Taraxacum officinale* agg. that were observed in cleared plots also by Fischer et al. (2002).

Although the herb-layer vegetation of dead wood stand was quite quickly enriched by pioneer and light demanding species like *Epilobium angustifolium* and *Rubus idaeus*, the communities otherwise held its former typical species, like *Trientalis europaea, Homogyne alpina, Soldanella montana, Oxalis acetosella*, and *Lycopodium annotinum* in dead wood stand. In contrast, these species stayed reduced in clearcut till 2009. These differences in species composition were finally demonstrated in the significant difference between dead wood stand and clearcut, answering the question that also the herb layer vegetation differed as the consequence of the additional disturbance caused by logging even after twelve years.

What is for the edaphically conditioned forests, the former composition is held (like dominating *Vaccinium myrthillus*), while some other species related either to outbreak like *E. angustifolium* or to climatically conditioned forests were newly observed in 2002 or 2009. This also indicates the longer resistance of waterlogged forests to bark beetle outbreak and its consequences like increased light conditions. Moreover, other species that slightly increased in waterlogged dead wood stand were *Calamagrostis villosa*, *Avenella flexuosa*, or some other species of climatically conditioned forests (similarly observed by Jonášová and Matějková, 2007; Wild et al., 2004). Also Neuhäuslová (2001b) noticed a shift to relatively drier types of vegetation in comparison with the 1950s.

In addition, the common change with time for all plot types was detected too, although it accounted for the lowest amount of variability. It could relate to some species that appeared newly for all plots, increased or decreased, while the reason could be the changed environmental conditions similar to all plots. Wild et al. (2004) compared the vegetation studies from 1970s and 1999 and observed the significant change in species composition of both the climatically and edaphically conditioned spruce forests but did not find any clear trend of changes in species composition, neither they were able to clarify the causal evidence for this temporal trend in understory vegetation. Among their finding the spreading of *Galium saxatile* was recorded in open forests or clearings in the Šumava Mts. in the late 1990s, while it was missing in the 1970s. We also observed *G. saxatile* to be favoured since the forest die-back as it increased at first in climatically conditioned stands, but in the waterlogged stands with some delay (this study).

Out of altogether 46 herb species, some species endangered to various extent (Grulich, 2012; Lepší et al., 2013) were observed within the twelve years of the study. While *Juncus squarrosus* (at one plot, only in 2002) and *Luzula campestris* agg. - *L. sudetica* (at one plot, in 2009) were recorded in clearcut; *Lycopodium annotinum* did not seem to be favoured by the conditions within clearcut. In contrast, plots without intervention successfully hosted rare species like *Lycopodium annotinum*, *Trientalis europaea*, *Soldanella montana*, or *Streptopus amplexifolius* (at one plot, only in 2002). Rare *Carex pauciflora* and *Dryopteris cambrensis* (Ekrt et al., 2010), were observed in waterlogged dead wood stand for the first time in 2009.

4.3 Conclusions

After the bark beetle attacks, mature spruce trees die back, gradual change of conditions takes place, and crucial components of biological legacies are maintained, so that both tree and herb layer proceed to direct recovery of the original tree species. The climatically conditioned and edaphically conditioned spruce forest continue to differ in its herb layer and the recovery progress is partially delayed in case of the waterlogged stands that were resistant to bark beetle attacks for longer time during the outbreak in the late 1990s.

After the dual disturbance, however, the youngest advance regeneration in clearcuts was significantly eliminated (Jonášová and Prach, 2004) and previous herb layer mechanically damaged during the clearing operations what also subsequently changed the microclimatic conditions of the sites. As a result, rare species became even rarer or missing, pioneer species occurred, and common grasses expanded several years after the events. New forest structure and composition is now, nevertheless, influenced by artificial regeneration (spruce and much less rowan); and spruce proved fast growth in clearcuts. Nevertheless, the height structure was consequently affected and the seedlings and saplings of lower categories were almost not observed the twelfth year after the events. Light-demanding pioneer tree species were still present, although not dominating. In conclusion, the changes caused by the additional disturbance in form of logging operations were apparent even twelve years after.

In contrast to negative consequences of salvage logging (e.g., Lindenmayer et al., 2008), the spontaneous development of the disturbed forest leaves the biological legacies that can help to restore the forest structures that are often limited in forests influenced by logging (like dead wood, Svoboda et al., 2010, etc.). Their importance for the regeneration (e.g., Bače et al., 2012) or also other organisms (Bässler et al., 2010; Lehnert et al., 2013; Müller et al., 2010; Pouska et al., 2011) shows that keeping them in the disturbed forest by spontaneous development of the ecosystem, historically human induced impacts can be at least partly repaired and the biodiversity enhanced. Long time span of such processes needs to be kept in mind, however, the national parks are right that areas where the spontaneous development should be allowed for unlimited time.

Appendices

*Appendix I. Numbers of tree species per 0.04 ha plot in three types of plot and years presented as total numbers and numbers in four height categories: I) < 50 cm, II) 50 – 100 cm, III) 100 – 200 cm, IV) ≥ 200 cm. Values were calculated as means (up) and medians (bellow) for dead wood stand (8 plots), clearcut (5 plots till 2002 and 4 plots in 2009), waterlogged dead wood stand (5 plots). In 2009, planted trees were included to the numbers in clearcut. Means and medians were rounded to the whole numbers; values lower than 1 tree per plot were denoted by "+"; the absence of a species was denoted by a dot. Nomenclature was unified according to Kubát et al. (2002). * birch –Betula* cf. *pubescens; ** willow – Salix* cf. *aurita.*

	Dead wood stand			Clearcut			Waterlogged dead wood stand		
	1998	2002	2009	1998	2002	2009	1998	2002	2009
	723	289	157	192	81	156	340	88	90
Norway spruce (*Picea abies*)	358	100	121	80	39	115	320	45	74
I	715	271	60	190	56	12	335	82	56
	348	84	31	76	23	8	319	43	41
II	4	13	62	2	19	20	2	3	23
	4	12	52	.	16	16	2	3	11
III	3	5	32	1	6	53	2	3	8
	1	4	32	.	2	44	1	1	1
IV	.	.	4	.	.	71	.	.	2
	.	.	2	.	.	55	.	.	1
	6	14	9	2	4	10	2	2	3
Rowan (*Sorbus aucuparia*)	4	13	8	2	4	10	.	2	2
I	5	7	2	2	1	6	2	1	2
	4	5	2	2	1	4	.	.	1
II	1	5	6	+	1	3	+	1	1
	.	5	4	.	2	3	.	1	1
III	.	2	2	.	1	2	.	+	+
	.	2	2	.	.	.	.	.	.
	.	.	+	1	1	3	.	15	17
Birch (*Betula* sp.)*	.	.	.	.	1	2	.	.	1
I	.	.	.	1	1	2	.	15	9
	.	.	.	.	.	1	.	.	1
II	.	.	+	.	1	+	.	.	6
	.	.	.	.	.	.	.	.	.
III	.	.	.	.	.	1	.	.	2
	.	.	.	.	.	1	.	.	.
	.	.	.	2	3	1	.	+	.
Willow (*Salix* sp.)**	.	.	.	.	2	1	.	.	.
I	.	.	.	2	2	+	.	+	.
	.	.	.	.	2	.	.	.	.
II	.	.	.	.	+	1	.	.	.
	.	.	.	.	.	.	.	.	.
	.	.	.	1	1	1	.	.	.
Aspen (*Populus tremula*)	.	.	.	.	1	1	.	.	.
I	.	.	.	1	1	1	.	.	.
	.	.	.	.	1	1	.	.	.
II	.	.	.	.	+	+	.	.	.
	.	.	.	.	.	.	.	.	.
	+	+	.	.	.	.	.	+	.
Beech (*Fagus sylvatica*)	.	.	.	.	.	.	.	.	.
I	+	+	.	.	.	.	.	+	.
	.	.	.	.	.	.	.	.	.

*Appendix II. Covers (%) of herb species per 0.04 ha plot in three types of plot and years. Values were calculated as means (up) and medians (bellow) for dead wood stand (8 plots), clearcut (5 plots till 2002 and 4 plots in 2009), waterlogged dead wood stand (5 plots). Values lower than 1 % were denoted by "+"; the absence of a species was denoted by a dot. Nomenclature was unified according to Kubát et al. (2002), except * Dryopteris cambrensis (Fraser-Jenkins) Beitel & W. Buck (determined by Libor Ekrt). ** Luzula campestris* agg. – cf. *sudetica.*

	Dead wood stand			Clearcut			Waterlogged dead wood stand		
	1998	2002	2009	1998	2002	2009	1998	2002	2009
Agrostis canina	.	.	.	+	.	.	+	+	1.2
				.			.	+	.
Agrostis capillaris	.	.	.	+	.	.	.	.	.
				.					
Athyrium distentifolium	+	+	+	.	.	.	.	.	+
	.	.	+						+
Avenella flexuosa	26.5	15.0	13.8	21.6	26.5	27.0	2.8	6.5	5.2
	28.8	13.8	15.3	22.5	30.0	28.1	+	5.0	5.3
Bistorta major	.	+	+	.	.	.	.	.	.
		.	.	.	.	.	.	.	.
Calamagrostis villosa	29.6	40.7	38.4	29.2	49.6	28.6	1.3	3.4	2.3
	34.8	44.4	38.8	20.5	48.8	26.3	.	+	+
Carex canescens	.	.	.	1.2	2.5	1.0	+	1.1	1.3
	.	.	.	+	2.0	.	.	+	+
Carex echinata	.	.	.	+	3.5	+	1.2	2.1	1.2
	.	.	.	.	.	.	+	+	+
Carex nigra	+	+	.	.	.	.	+	+	1.8
	.	.	.	.	.	.	+	+	.
Carex ovalis	.	.	.	.	.	+	.	.	.
	.	.	.	.	.	+	.	.	.
Carex pauciflora	.	.	.	.	.	.	.	.	+
	.	.	.	.	.	.	.	.	.
Carex rostrata	.	.	.	.	.	.	1.1	+	+
	.	.	.	.	.	.	.	.	+
Carex sp.	.	.	.	.	.	.	1.3	.	.
	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa	.	.	.	.	+	+	.	+	+
	.	.	.	.	.	.	.	.	.
*Dryopteris cambrensis**	.	.	.	.	.	.	.	.	+
	.	.	.	.	.	.	.	.	.
Dryopteris dilatata	2.0	2.5	1.2	+	+	+	+	+	1.1
	1.0	2.1	1.1	+	+	+	+	+	1.4
Dryopteris filix-mas	.	.	+	.	.	+	.	.	+
	.	.	.	.	.	.	.	.	.
Epilobium angustifolium	+	+	+	+	+	+	.	+	1.0
	+	+	+	+	+	+	.	.	+
Epilobium sp.	.	.	.	.	.	.	.	+	.
	.	.	.	.	.	.	.	.	.
Eriophorum vaginatum	.	.	.	.	.	.	8.3	8.5	4.6
	.	.	.	.	.	.	5.5	7.5	2.3
Galeopsis bifida	.	.	+	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.
Galium saxatile	+	+	2.4	+	+	2.8	.	+	+
	+	+	1.1	.	+	1.4	.	.	.
Hieracium subg. *Hieratium*	.	.	.	+	+	+	.	.	.
	.	.	.	.	.	.	.	.	.
Homogyne alpina	+	+	+	.	.	+	+	+	+
	+	+	+	.	.	.	.	.	.
Juncus effusus	.	.	.	+	+	+	.	.	.
	.	.	.	.	.	.	.	.	.
Juncus filiformis	.	.	.	.	+	2.8	+	.	+
	.	.	.	.	.	.	.	.	.
Juncus squarrosus	.	.	.	.	+	.	.	.	.
	.	.	.	.	.	.	.	.	.
Luzula campestris agg.**	.	.	.	.	.	+	.	.	.
	.	.	.	.	.	.	.	.	.
Luzula sylvatica	9.1	2.8	+	5.2	3.4	10.6	.	.	+
	6.6	2.4	+	7.3	3.1	7.3	.	.	.

Lycopodium annotinum	+	+	+	+	+	+	+	+	+
	.	.	.	+	+	+	.	.	.
Maianthemum bifolium	+	+	+	+	+	+	.	.	.
	.	.	.	.	.	+	.	.	.
Molinia caerulea	.	.	+	.	.	+	5.0	5.6	2.5
	.	.	.	.	.	.	1.3	1.0	+
Nardus stricta	.	.	.	.	.	.	+	+	.
	.	.	.	.	.	.	.	.	.
Oxalis acetosella	1.0	2.8	+	+	+	+	+	+	+
	+	1.9	+	+	+	.	.	.	.
Polygonatum verticillatum	+	+	+	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.
Prenanthes purpurea	+	+	+	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.
Rubus idaeus	+	+	+	+	1.3	+	.	+	+
	.	+	+	+	+	+	.	.	+
Rumex acetosa	.	.	.	.	+	.	.	.	.
	.	.	.	.	.	.	.	.	.
Rumex acetosella	.	.	.	+	+	+	.	.	.
	.	.	.	.	.	.	.	.	.
Senecio nemorensis agg.	.	.	+	.	.	+	.	.	.
	.	.	.	.	.	.	.	.	.
Soldanella montana	+	+	+	.	+	+	.	.	.
	+	.	.	.	.	.	.	.	.
Streptopus amplexifolius	.	+	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.
Taraxacum sect. *Ruderalia*	+	+	.	+	+	.	.	.	.
	.	.	.	+	.	.	.	.	.
Trientalis europea	+	1.4	+	+	.	+	+	+	+
	+	1.4	+	.	.	.	.	+	+
Vaccinium myrtillus	14.4	9.9	9.3	1.9	2.1	4.1	25.3	30.1	26.8
	4.4	4.1	3.7	+	+	+	32.5	32.5	35.5
Vaccinium vitis-idea	.	+	+	.	.	.	+	+	+
	.	.	.	.	.	.	+	+	+

Appendix III. Covers (%) of particular vegetation layers (tree canopy includes live and dead standing trees and snags) or surface cover (wood includes logs and stumps) per 0.04 ha plot in three types of plot and years. Percentage covers of the surviving trees in the canopy were presented for 2009. Values were calculated as means (up) and medians (bellow) for dead wood stand (8 plots), clearcut (5 plots till 2002 and 4 plots in 2009), waterlogged dead wood stand (5 plots). Values lower than 1 % were denoted by "+"; the absence was denoted by a dot.

	Dead wood stand			Clearcut			Waterlogged dead wood stand		
	1998	2002	2009	1998	2002	2009	1998	2002	2009
Moss layer	18.5	11.5	17.1	3.9	7.1	12.8	46.5	39.0	51.4
	16.8	11.0	11.1	3.3	7.5	10.3	43.8	37.5	47.5
Herb layer	78.0	73.6	69.3	59.5	88.9	80.0	46.6	57.6	53.8
	78.8	73.1	70.0	63.8	88.8	81.9	53.8	65.0	56.3
Shrub layer	+	+	2.5	.	.	10.5	1.1	1.3	1.2
	+	+	2.3	.	.	6.8	+	+	1.0
Tree canopy	37.0	11.4	1.7	.	.	+	50.0	28.5	6.8
	35.0	10.8	1.4	.	.	.	48.8	26.3	2.8
- live			+			.			2.7
			+			.			+
Wood	2.7	5.2	18.7	1.6	4.1	4.3	1.6	4.3	14.1
	2.9	3.5	18.9	+	3.8	3.9	1.5	5.3	15.5
Litter	7.9	3.8	2.1	31.8	2.9	2.4	15.1	11.5	11.0
	7.8	2.3	2.0	33.8	2.5	1.9	10.5	4.3	3.3
Soil surface	.	.	+	+	1.6	1.1	.	.	+
	.	.	.	.	+	+	.	.	+

References

Bače, R., Janda, P., Svoboda, M., 2009. Vliv mikrostanoviště a horního stromového patra na stav přirozené obnovy v horském smrkovém lese na Trojmezné [Effect of microsite and upper tree layer on natural regeneration in the mountain spruce forest stand Trojmezná (Šumava National Park)]. Silva Gabreta 15, 67-84 (in Czech, English Summary).

Bače, R., Svoboda, M., Pouska, V., Janda, P., Červenka, J., 2012. Natural regeneration in Central-European subalpine spruce forests: Which logs are suitable for seedling recruitment? Forest Ecology and Management 266, 254-262.

Bässler, C., Müller, J., 2010. Importance of natural disturbance for recovery of the are polypore *Antrodiella citrinella* Niemelä & Ryvarden. Fungal Biology. 114, 129-133.

Bässler, C., Müller, J., Svoboda, M., Lepšová, A., Hahn, C., Holzer, H., Pouska, V., 2012. Diversity of wood-decaying fungi under different disturbance regimes – a case study from spruce mountain forests. Biodiversity and Conservation 21, 33-49.

Beneš, J., 1995. Les a bezlesí. Vývoj synantropizace české části Šumavy - Wald und abgerodete Landschaft. [Die Entwicklung der synanthropischen Processe in böhmischen Teil des Böhmerwaldes]. Zlatá stezka. Sborník Prachatického muzea *2*, 11-33 (in Czech with German summary).

Brůna, J., Wild, J., Svoboda, M., Heurich, M., Müllerová, J., 2013. Impacts and underlying factors of landscape-scale, historical disturbance of mountain forest identified using archival documents. Forest Ecology and Management 305, 294-306.

Čada, V., Svoboda, M., Janda, P., 2013. Dendrochronological reconstruction of the disturbance history and past development of the mountain Norway spruce in the Bohemian Forest, central Europe. Forest Ecology and Management 295, 59-68.

Čeřovský, J., Podhajská, Z., Turoňová, D. (Eds.), 2007. Botanicky významná území ČR. AOPK ČR, Praha, (in Czech).

Chábera, S. (Ed.), 1987. Příroda na Šumavě [Nature of the Bohemian Forest]. Jihočeské nakladatelství. České Budějovice, (in Czech).

Čížková, P., 2010. Biomonitoring lesních ekosystémů v území NP Šumava ponechaném samovolnému vývoji. Zpráva o výsledcích zpracování dat projektu 19/CIZ/3/46/2007. Správa NP a CHKO Šumava, Vimperk (in Czech).

Čížková, P., Svoboda, M., Křenová, Z., 2011. Natural regeneration of acidophilous spruce mountain forests in non-intervention management areas of the Šumava National Park – the first results of the Biomonitoring project. Silva Gabreta 17, 19-35.

Czech Geological Survey, 2012. Ministry of the Environment of the Czech Republic. Viewed 31st October 2012, <http://maps.geology.cz/geocr_25/ >

Ekrt, L., Štech, M., Lepší, M., Boublík, K., 2010. Rozšíření a taxonomická problematika skupiny *Dryopteris affinis* v České republice [Distribution and taxonomy of the *Dryopteris affinis* group in the Czech Republic]. Zprávy České Botanické Společnosti 45, 25-52 (in Czech, English Summary).

Fischer, A., Lindner, M., Abs, C., Lasch, P., 2002. Vegetation dynamics in Central European forest ecosystem (near-natural as well as managed) after storm events. Folia Geobotanica 37, 17-32.

Foster, D.R., Orwig, D.A., 2006. Preemptive and Salvage Harvesting of New England Forests: When Doing Nothing Is a Viable Alternative. Conservation Biology 20, 959–970.

Frelich, L.E., 2002. Forest Dynamics and Disturbance Regimes. Cambridge University Press, Cambridge.

Grulich, V., 2012. Red List of vascular plants of the Czech Republic: 3rd edition. Preslia 84, 631–645.

Hais, M., Jonášová, M., Langhammer, J., Kučera, T., 2009. Comparison of two types of forest disturbance using multitemporal Landsat TM/ETM+ imagery and field vegetation data. Remote Sensing of Environment 113, 835-845.

Heurich, M., 2001. Waldentwicklung im montanen Fichtenwald nach großflächigem Buchdruckerbefall im Nationalpark Bayerischer Wald. In: Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall. Nationalpark Bayerischer Wald. - Wissenschaftliche Reihe 14, 99-177 (in German, English Summary).

Heurich, M., 2009. Progress of forest regeneration after a large-scale *Ips typographus* outbreak in the subalpine *Picea abies* forest of the Bavarian National Park. Silva Gabreta 15, 49-66.

Heurich, M., Reinelt, A., Fahse, L., 2001. Die Buchdruckermassenvermehrung im Nationalpark Bayerischer Wald. In: Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall. Nationalpark Bayerischer Wald, Wissenschaftliche Reihe 14, 9-48 (in German, English Summary).

Ilisson, T., Köster, K., Vodde, F., Jõgiste, K., 2007. Regeneration development 4-5 years after a storm in Norway spruce dominanted forests, Estonia. Forest Ecology and Management 250, 17-24.

Jakuš, R., Edwards-Jonášová, M., Cudlín, P., Blaženec, M., Ježík, M., Havlíček, F., Moravec, I., 2011. Characteristics of Norway spruce trees (*Picea abies*) surviving a spruce bark beetle (*Ips typographus* L.) outbreak. Trees 25, 965-973.

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 (in German, English Summary).

Jelínek, J., 1988. Větrná a kůrovcová kalamita na Šumavě z let 1868 až 1878 [Wind- and bark-beetle calamity in the Bohemian Forest from 1868 to 1878]. Ms., Lesprojekt, Brandýs nad Labem (in Czech).

Jonášová, M., Matějková, I., 2007. Natural regeneration and vegetation changes in wet spruce forests after natural and artificial disturbances. Canadian Journal of Forest Research 37, 1907-1914.

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.

Jonášová, M., Prach, K., 2008. The influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests. Biological Conservation 141, 1525-1535.

Jonášová, M., Vávrová, E., Cudlín, P., 2010. Western Carpathian mountain spruce forest after a windthrow: Natural regeneration in cleared and uncleared areas. Forest Ecology and Management 259, 1127-1134.

Kubát, K., Hrouda, L., Chrtek, Jr. J., Kaplan, Z., Kirschner, J., Štepánek, J. (Eds.), 2002. Klíč ke květeně České republiky, first ed. Academia. Praha (in Czech).

Kupferschmid, A.D., Brang, P., Schönenberger, W., Bugmann, H., 2006. Predicting tree regeneration in *Picea abies* snag stands. European Journal of Forest Research 125, 163-179.

Kupferschmid, A.D., 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.

Kuuluvainen, T., 2002. Natural Variability of Forests as a Reference for Restoring and Managing Biological Diversity in Boreal Fennoscandia. Silva Fennica 36, 97-125.

Lehnert, L.W., Bässler, C., Brandl, R., Burton, P.J., Müller, J., 2013. Conservation value of forests attacked by bark beetles: Highest number of indicator species is found in early successional stages. Journal for Nature Conservation 21, 97-104.

Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Ecological Data using Canoco. Cambridge University Press.

Lepší, P., Lepší, M., Boublík, K., Štech, M., Hans, V. (Eds.), 2013. Červená kniha květeny jižní části Čech. Jihočeské muzeum v Českých Budějovicích (in Czech, English Summary).Lindenmayer, D.B., Burton, P.J., Franklin, J.F., 2008. Salvage logging and its ecological consequences. Island Press. Washington.

Mayer, P., Abs, C., Fischer, A., 2004. Colonisation by vascular plants after soil disturbance in the Bavarian Forest – key factors and relevance for forest dynamics. Forest Ecology and Management 188, 279-289.

Moravec, J., Husová, M., Jirásek, J., 2002. Vegetation Survey of the Czech Republic. Coniferous Forests, vol. 3. Academia, Praha.

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 191, 139-150.

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. Biodiversity and Conservation 17, 2979-3001.

Müller, J., Noss, R.F., Bussler, H., Brandl, R., 2010. Learning from a "benign neclect strategy" in a national park: Response of saproxylic beetles to dead wood accumulation. Biological Conservation 143, 2559-2569.

Neuhäuslová, Z. (Ed.), 2001a. The Map of Potential Natural Vegetation of the Šumava National Park. Silva Gabreta, Supplementum 1. Správa NP Šumava. Vimperk.

Neuhäuslová, Z., 2001b. Diverzita a dynamika vegetace NP Šumava, in: Mánek, J. (Ed.), Aktuality šumavského výzkumu [Research Actualities in Bohemian/Bavarian forest], Srní (CZ), 2-4 April 2001, Správa NP a CHKO Šumava, Vimperk, pp. 48 – 50.

Palmer, M., Smart, J., 2001. Important Plant Areas in Europe. Guidelines for the Selection of Important Plant Areas in Europe. Plantlife, London.

Pouska, V., Lepš, J., Svoboda, M., Lepšová, A., 2011. How do log characteristics influence the occurrence of wood fungi in a mountain spruce forest? Fungal Ecology 4, 201-209.

Pralesy.cz, 2004. VÚKOZ, v.v.i., Department of Forest Ecology, Brno. Viewed 15th November 2013, <http://www.pralesy.cz/?id=6818>

Sádlo, J., 2001. Primární bezlesí na Šumavě, in: Mánek, J. (Ed.), Aktuality šumavského výzkumu [Research Actualities in Bohemian/Bavarian forest], Srní (CZ), 2-4 April 2001, Správa NP a CHKO Šumava, Vimperk, pp. 46 – 47 (in Czech).

Šantrůčková, H., Šantrůček, J., Šetlík, J., Svoboda, M., Kopáček, J., 2007. Carbon isotopes in tree rings of Norway spruce exposed to atmospheric pollution. Environmental Science and Technology, 41, 5778-5782.

Schelhaas, M. J., Nabuurs, G. J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology 9, 1620-1633.

Svoboda, M., Fraver, S., Janda, P., Bače, R., Zenáhlíková, J., 2010. Natural development and regeneration of a Central European montane spruce forest. Forest Ecology and Management 260, 707-714.

Svoboda, M., Janda, P., Nagel, T. A., Fraver, S., Rejzek, J., Bače, R., 2012. Disturbance history of an old-growth sub-alpine *Picea abies*stand in the Bohemian Forest, Czech Republic. Journal of Vegetation Science 23, 86–97.

Svoboda, M., Pouska, V., 2008. Structure of a Central-European mountain spruce old-growth forest with respect to historical development. Forest Ecology and Management 255, 2177-2188.

Ter Braak, C.J.F., Šmilauer, P., 2009. Canoco for Windows, version 4.56, computer programme, Biometris – Plant Research International, Wageningen, The Netherlands.

Tolasz, R. et al, 2007. Altas podnebí Česka [Climate Atlas of Czechia]. Český hydrometeorologický ústav, Universita Palackého, Olomouc. Praha.

Wild, J., Neuhäuslová, Z., Sofron, J., 2004. Changes of plant species composition in the Šumava spruce forests, SW Bohemia, since the 1970s. Forest Ecology and Management 187, 117-132.

Zatloukal, V., 1998. Historické a současné příčiny kůrovcové kalamity v Národním parku Šumava [Historical and current factors of the bark beetle calamity in the Šumava National Park]. Silva Gabreta 2, 327-357.

Zenáhlíková, J., Svoboda, M., Wild, J., 2011. Stav a vývoj přirozené obnovy před a jeden rok po odumření stromového patra v horském smrkovém lese na Trojmezné v Národním parku Šumava [The state and development of natural regeneration before and one year after a dieback in the tree layer of a mountain spruce forest in the Trojmezná area of the Šumava National Park]. Silva Gabreta 17, 37-54 (in Czech, English Summary).

Zielonka, T., 2006. When does dead wood turn into a substrate for spruce replacement? Journal of Vegetation Science 17, 739-746.

Żywiec, M., Ledwoń, M., 2008. Spatial and temporal patterns of rowan (*Sorbus aucuparia* L.) regeneration in West Carpathian subalpine spruce forest. Plant Ecology 194, 283-291.