Forest succession after a major anthropogenic disturbance: a case study of the Jewish Forest in the Bohemian Forest, Czech Republic

J. Bednařík[1], V. Čada[1], K. Matějka[2]

[1]*Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic*

[2]*IDS, Prague, Czech Republic*

ABSTRACT: The knowledge of forest development after disturbances, particularly anthropogenic disturbances, is of major importance for forest management. Many areas of mountain forests in Europe have been affected by human activities such as felling and livestock grazing in the past and then left for natural succession. Those forests provide several ecosystem services (e.g. soil or avalanche protection) and therefore it is vital to know their developmental processes. The Norway spruce forest stand in the area of Medvědí Mt. (Šumava National Park, Czech Republic), known as the Jewish Forest, is considered an example of succession after anthropogenic disturbances. This study aimed to: (1) analyse the history of disturbances which affected the locality, (2) describe the subsequent process of forest succession which led to the development of the present forest formation. We conducted a dendrochronological analysis and a spatial analysis. The main cohort was established after a period of disturbances in the first half of the 20th century. Both natural (windstorm) and anthropogenic (logging and livestock grazing) disturbances coincided during this period. Regeneration of low density was restricted to a short period after the disturbance and was likely dependent on the occurrence of proper microsites. Later, regeneration was probably obstructed by lack of convenient microsites and high competition of the herb layer. Nowadays, new regeneration emerges together with proper microsite at decaying wood and near mature trees. We conclude that anthropogenic disturbances can limit the density and heterogeneity of regeneration, which leads to the establishment of sparse stand. This structure can persist for decades before proper microsites accumulate and enable regeneration.

Keywords: dendroecology; disturbance history; grazing; logging; *Picea abies* (L.) Karst.; spatial structure

Communities undergo various changes during the development after a disturbance. The process of change in species composition and stand structure is usually referred to as succession. Mountain spruce forests in Central Europe have recently suffered several major disturbances which have given rise to many questions concerning their natural dynamics. The latest studies showed that disturbances, even the large-scale and severe ones, are an integral part of mountain spruce forest dynamics (Zielonka, Malcher 2009; Zielonka et al. 2010; Čada, Svoboda 2011; Panayotov et al. 2011; Svoboda et al. 2012; Čada et al. 2013). Spruce is able to regenerate after an extensive disturbance (Heurich 2009; Kindlmann et al. 2012) and become the dominant tree species immediately after a severe disturbance (Fischer et al. 2002; Jonášová, Prach 2008). In natural conditions, the spruce forms advanced regeneration that grows to the canopy after disturbance (Jonášová, Matějková 2007; Heurich 2009; Čížková et al. 2011).

The structure and dynamics of spruce forests which have been disturbed by human activities such as felling and livestock grazing have been subjected to relatively minor attention, particularly outside the Alps (Motta et al. 1999, 2002), even though these activities used to be common

throughout Central Europe. Anthropogenic disturbances such as felling are often more severe than natural wind or bark beetle disturbances; they often damage advanced regeneration and disturb the soil to a larger extent (Jonášová, Matějková 2007; Jonášová et al. 2010). After logging, the cover of the moss species decreases and grasses, such as *Calamagrostis villosa* and *Deschampsia flexuosa*, expand (Vacek et al. 1999; Kooijman et al. 2000; Fischera et al. 2002; Jonášová, Prach 2004, 2008; Jonášová, Matějková 2007; Vávrová, Cudlín 2010). Livestock grazing can further reduce the tree regeneration and obstruct the forest succession (Svoboda 1952).

Reduction of livestock grazing has led to reforestation of many pastures at high altitudes (Freléchoux et al. 2007; Janišová et al. 2007; Tasser et al. 2007; Lingua et al. 2008; Pornaro et al. 2013) as well as meadows at a wide range of altitudes (Blažková 1988, 1991, 2003). Still, non-forest areas do not often offer favourable conditions for seedlings of woody plants, because seedlings have to cope with intense competition of herbs (Prach et al 1996; Castro et al. 2002; Gömöry 2006; Vandenberghe et al. 2006; Dovčiak et al. 2008) or with a thick layer of undecomposed litter (Prach et al. 1996). In some cases, extensive grazing may provide gaps for tree establishment, disrupting the herb cover and removing the litter (Gömöry et al. 2006; Rosenthal 2010). Colonisation of non-forest areas is also facilitated by certain herb layer species which are not browsed by animals and thus provide shelter for seedlings (Smit et al. 2005), or by the trees that have grown before the discontinuation of grazing. As soon as the intensity of grazing decreases or the grazing ends, new individuals begin to emerge in the immediate vicinity of these trees (Lingua et al. 2008). Mature trees improve conditions for regeneration around them by increasing density of seed rain, influencing microclimate, reducing competition of grasses and changing litter and soil conditions (Finegan 1984; Miller, Halpern 1998; Gömöry et al. 2006; Janišová et al. 2007; Dovčiak et al 2008; Halpern et al. 2010). At higher altitudes, they also affect thickness of snow cover, and they offer mechanical support and protection from herbivores (Lingua et al. 2008). As a result, new individuals grow close to older trees and create clusters (Miller, Halpern 1998; Baumeister, Callaway 2006; Gömöry et al. 2006; Halpern et al. 2010). Open areas between scattered individuals or patches of existing trees are filled in the following phases of succession (Lingua et al. 2008). As the canopy density gradually increases, the process of facilitation may turn into competition (Gömöry et al. 2006; Halpern

et al. 2010). The increase in competition explains changes from aggregated to regular spatial pattern during succession (Gömöry et al. 2006). It points to the fact that all three models of succession (facilitation, tolerance and inhibition; Connell, Slatyer 1977) are applicable in the forests.

The succession of woody plants in meadows at higher altitudes where the spruce (*Picea abies* [L.] Karst.) is a dominant woody species, usually advances from the forest stand edge where the seed density is highest and the growth of new seedlings is promoted by the individuals of the tree layer; these provide shading and improve the overall site conditions (Hughes et al. 1997; Dovčiak et al. 2005; Tasser et al. 2007; Doubková 2008; Halpern et al. 2010). The spruce is an anemochorous species and as such it has a greater colonisation potential than woody plants with different expansion strategies (Prach 1994; Dostálová 2009). This holds even though maximum seed deposition occurs – depending on the fecundity and height of the tree – within only 0.5 to 2.1 m from the reproducing tree and then it rapidly decreases with the distance, and the mean dispersal distance thus remains within the range of 4.3–17.4 m (Dovčiak et al. 2008). The last part of the meadow ecosystem to be invaded by woody plants is the very centre (owing to lack of seeds and direct sunlight) where the trees largely establish only after favourable climatic conditions arise which influence the competition between seedlings of woody species and herbs (Dovčiak et al. 2005; Halpern et al. 2010).

Our study focuses on the description of forest succession after disturbance in the so-called Jewish Forest in the Bohemian Forest (Czech Republic). Our specific goals include:
– an analysis of the history of disturbances (their extent, timing and severity), which are not sufficiently described by historical sources – the forest stand was logged in the mid-19th century, left without artificial reforestation and used as a pasture for several decades (Ministr 1963; Vicena 2011),
– a description of the subsequent succession which led to the development of the present forest formation. We expect that the subsequent succession proceeded as gradual colonisation of open areas between scattered (remnant) individuals or patches of trees, which facilitated establishment of new seedlings.

The research examined the structure of the tree layer using spatial analysis and the history of disturbances using dendrochronological methods.

MATERIAL AND METHODS

Study area. The Jewish Forest is situated on Medvědí Mt. (1,224 m a.s.l.; 48°59'39.416"N, 13°25'37.809"E), which is located in the central part of the Šumava National Park, on the border with Germany (Fig. 1). The bedrock is dominated by the Moldanubian rock series (mostly schist gneiss, paragneiss, and composite gneiss) (Babůrek et al. 2006). The soil cover consists mostly of haplic and entic podzols, histosols and marginally also gleysols (Kozák et al. 2009). The mean annual temperatures in the area range between 2 and 3°C and the mean annual precipitation exceeds 1,200 mm (Tolasz et al. 2007). The potential vegetation is classified as *Calamagrostio villosae-Piceetum*, *Mastigobryo-Piceetum* and *Sphagno-Piceetum* (Neuhäuslová, Moravec 1998).

The distinctive structure of the Jewish Forest is park-like, with solitary trees and clusters of trees. The amount of natural regeneration is low, mainly due to high density of ground vegetation and lack of suitable microsites for regeneration. Farther from the summit, the tree vegetation grows denser and assumes the character of a closed forest (Bednařík, Matějka 2014).

The Jewish Forest is characterised by the typical opened forest structure (Fig. 1) rather than by the exact geographical position. Nowadays, the Jewish Forest lies within two historically different areas with different management practices. Initially, according to the historical sources, Jewish forest was a synonym for Roklan cameral forest (in the second part of the 19th century). It had developed in the process of secondary succession after the exploitation of the Roklan cameral forest in 1846 to 1847. The area was not artificially reforested after logging and was used for forest fruit picking and livestock grazing (Ministr 1963; Vicena 2011). Available materials do not allow determining the magnitude and duration of logging and grazing. The area of interest was later probably affected by the wind disturbances in 1928 and 1929 (Ministr 1963). In the same period, Klečka (1930) depicted the area as a new clearing created by wind and used for livestock grazing and described the grassland communities as dominated by *Nardus stricta*. Since the early 20th century the typical park-like forest structure of Jewish forest was found also in the eastern part of Medvědí Mt. in the area of the former Prášily domain, where there were dense forest stands before (Jelínek 2005). Planting of new trees was done in the 1970s in a part of the most open stands around the summit of Medvědí Mt. (NP Šumava Archives, Kašperské Hory; Forest management plan Srní 1969–1978, Javoří Pila forest district).

Data collection. A total of 10 research plots were established in the central part of the study area (Fig. 1, Table 1) along the gradient from dense to open stands to describe different stages of forest succession. Each plot was a square of 50 × 50 m, spaced about 200 m apart. The plots extended to the west (5 plots representing the area of the Roklan cameral forest), to the east and to the north (3 and 2 plots, respectively, in the former Prášily domain) from Medvědí Mt.'s summit. Plots B1, B2 and B3 can be characterised as open forest stands, B5, B7, B9 and B10 as dense forests.
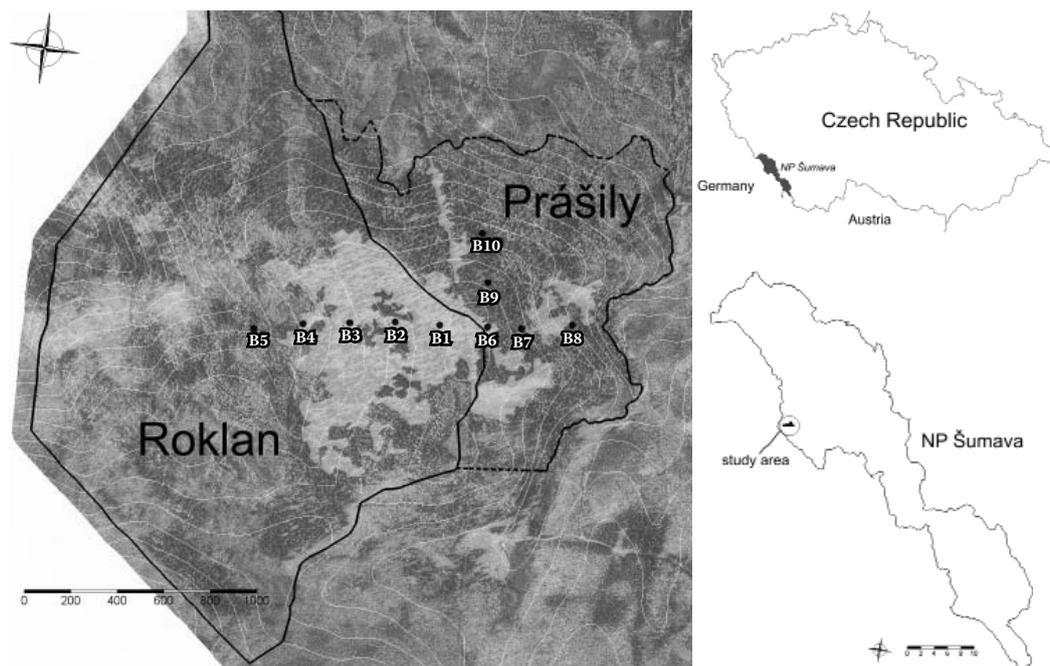
Fig. 1. The area of interest. Grey lines represent contours with 10 m interval. The area of low tree density is light

Table 1. Basic characteristics of the research plots (Bednařík, Matějka 2014)

Plot	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10
Elevation (m)	1,217	1,205	1,186	1,172	1,158	1,220	1,203	1,174	1,209	1,185
Slope (°)	2	5	5	3	6	2	6	20	5	4
Aspect	SW	W	SW	W	N	ENE	ENE	NE	NE	N
Average air temperature (°C)[1]	3.5	3.6	3.7	3.8	3.7	3.4	3.5	3.6	3.4	3.4
Forest site type (Průša 2001)	8M3	8M3	7K1/8G3	8G3/7K1	8G3/8R1	8Z4/8M3	8M3/8K2	8K2	8M3	8M3/8K2
Ground vegetation cover (%)	90	90	95	80	85	80	90	85	85	85
Canopy cover (%)	4	30	25	15	54	20	28	43	34	56
Spruce seedlings < 0.1 m (ha^{-1})	0	44	0	212	260	4	0	20	4	184
Spruce saplings ≥ 0.1 m and < 1.3 m (ha^{-1})	4	72	40	1,380	812	96	12	84	76	88
Living trees ≥ 1.3 m (ha^{-1})	32	152	184	124	700	180	148	236	408	192
Dead trees ≥ 1.3 m (ha^{-1})	0	24	8	136	212	0	20	12	4	28
Lying deadwood (m^3·ha^{-1})	0	11.0	0	135.6	7.1	0	39.3	0.9	0	17.2

[1]Average temperature during 1961–1990 according to the model, the PlotOA software was applied (Kindlmann et al. 2012; www.infodatasys.cz/sumava/tvp.pdf)

Plots B4, B6 and B8 are on border between open and dense forest structure.

Stand structure was measured using the Field-Map technology (IFER Ltd., Strašice, Czech Republic). We recorded positions and species of living trees and dead trees (height ≥ 1.3 m) and saplings (height < 1.3 m). For living trees, we measured diameter at breast height (DBH), height, crown projection and height of living crown base. For standing dead trees, we measured DBH (or diameter at the highest point for shorter snags and stumps) and height. For saplings, we measured height.

Subsequently, we extracted increment cores from every eligible living and dead tree with DBH ≥ 10 cm at the height of 1.3 m. In addition, we cored eighteen randomly selected individuals with DBH < 10 cm. The increment cores were air-dried, attached to a wooden mount and cut with razor blade. The contrast was improved by moistening and impressing with chalk. Ring widths on all cores were measured to the nearest 0.01 mm using the sliding table LINTAB and TsapWin software (Rinntech, Heidelberg, Germany). Each tree-ring series was cross-dated following the procedure of Yamaguchi (1991) and using statistical tests implemented in PAST4 (Knibbe 2007). In cases where the core did not pass through the pith, the number of rings missed was estimated based on the

curvature and mean width of the five tree rings closest to the centre (Duncan 1989). We did not correct for bias caused by coring height (Niklasson 2002); therefore, the "age" mentioned hereafter is not the true age but the recruitment age at the coring height.

Finally, we obtained 430 growth series (plus 18 series of trees < 10 cm DBH). In 14 of them, it was not possible to determine the distance to the pith and so they were not included in all of the analyses. The pith was reached in 29% out of 448 samples. In 74% of them, the distance to the pith was within 10 mm.

Data analysis.

Analysis of disturbance history. Two types of events were assumed to indicate past disturbances: (1) the release from suppression (an abrupt, sustained and large increase in growth) which indicates the death of surrounding trees and (2) the gap origin (a rapid early growth rate) which indicates open conditions during the recruitment of the tree (Lorimer, Frelich 1989). Gap-originating trees were defined as trees whose mean width of the 6–15th ring exceeded 1.0 mm (Splechtna et al. 2005; Firm et al. 2009; Jönsson et al. 2009) and whose subsequent growth pattern was declining, parabolic, or flat (Frelich 2002). Releases from suppression were identified using the "ab-

solute increase" method (Fraver, White 2005; Čada, Svoboda 2011; Čada et al. 2013). Absolute growth changes were calculated for each year of each series (except for the first and last 10 years) by subtracting the prior 10-year mean from the subsequent 10-year mean. Release years were identified by a growth change value that was the maximum of the surrounding 20-year interval (± 10 yr) and that exceeded the threshold of +0.55 mm (Jönsson et al. 2009). This threshold was specified for the Norway spruce based on the experience with its growth variation (Jönsson et al. 2009). Finally, all of the series and their releases were visually checked and releases were excluded if the growth acceleration was not apparent (for more details see Čada, Svoboda 2011; Čada et al. 2013). Disturbance chronologies were calculated following Lorimer and Frelich (1989) and Frelich (2002). All release and gap-origin events were summarised by decades and plotted proportionally to sample depth at the end of the decade. Chronologies were truncated when sample depth dropped below 3. The resulting chronology, called "tree-population-based" chronology by Frelich (2002), shows the proportion of the population that indicates a disturbance in a given decade.

Spatial pattern analysis. Spatial analyses were performed merely for the Norway spruce due to the low proportion of other species in the research plots. Spruce trees were divided into two groups according to DBH. The first group included individuals with DBH < 10 cm, hereafter referred to as "regeneration"; and the second group included all trees (living and recently dead) with DBH ≥ 10 cm, hereafter referred to as "trees". We did not consider regeneration growing on dead wood, because we wanted to test the spatial patterning of trees not affected by the presence or absence of dead wood. Dead wood is the preferred microsite for spruce regeneration (Kupferschmidt, Bugmann 2005; Ulbrichová et al. 2006; Bače et al. 2009; Jonášová et al. 2010; Svoboda et al. 2010; Čížková el al. 2011) and its amount was inhomogeneous in the study area. Plots containing less than 15 individuals in any of the groups were not used for calculations. Therefore, plot 1 was not used for any spatial analysis and plot 7 was not used for the analysis of the spatial pattern of regeneration.

Spatial patterns within each group were evaluated using the pair correlation function $g(r)$ (Stoyan, Stoyan 1994), which is a transformation of Ripley's K-function (Ripley 1977). The pair correlation function was computed according to the Equation:

$$g(r) = K'(r)/2\pi r \qquad (1)$$

where:

$K'(r)$ – derivative of Ripley's K-function.

As the pair correlation function does not register an aggregated tree frequency with increasing distance but rather registers the changes in the frequency with increasing distance, it is more sensitive than the K-function, and also reveals small changes in the distribution pattern (Pretzsch 2009). For a Poisson distribution, the pair correlation function is equal to 1. Values $g(r) < 1$ suggest inhibition between points, values greater than 1 suggest clustering. To test the null hypothesis of random distribution of individuals, 999 Monte Carlo simulations were performed to generate 99% significance band. The null hypothesis was rejected when the observed function value deviated outside the simulated envelope. Ripley's isotropic correction was applied to reduce bias caused by the edge effect. The cross-type pair correlation function $g_{i,j}(r)$ was used to test the spatial dependence between trees and regeneration. The computations were conducted in the R software (R Core Team, Vienna, Austria) using the "spatstat" package (Baddeley, Turner 2005).

Moran's I coefficient (Moran 1950) was used to test the spatial autocorrelation of tree canopy accessions. Canopy accession was defined as the calendar year in which the tree started to grow to the canopy (i.e. gap origin or first release event). A correlogram where autocorrelation values are plotted in the ordinate against the distance (d) among the points was drawn for each plot, using the 5 m distance classes. Moran's coefficient generally varies from −1 to 1; positive values correspond to positive autocorrelation, negative values to negative autocorrelation and the value 0 indicates no spatial autocorrelation. The computations were carried out with the "ncf" package (Bjørnstad 2013) and the R software (R Core Team, Vienna, Austria).

RESULTS

Age structure

The present-day Norway spruce stand in the study area comes from three main population waves (Fig. 2). The most important one occurred between 1920 and 1959. Fifty-four percent of trees reached the coring height during this period (forty percent of trees were recruited in the 1930s and 1940s). The second important cohort appeared after 1980, contributing 27% of the current popu-
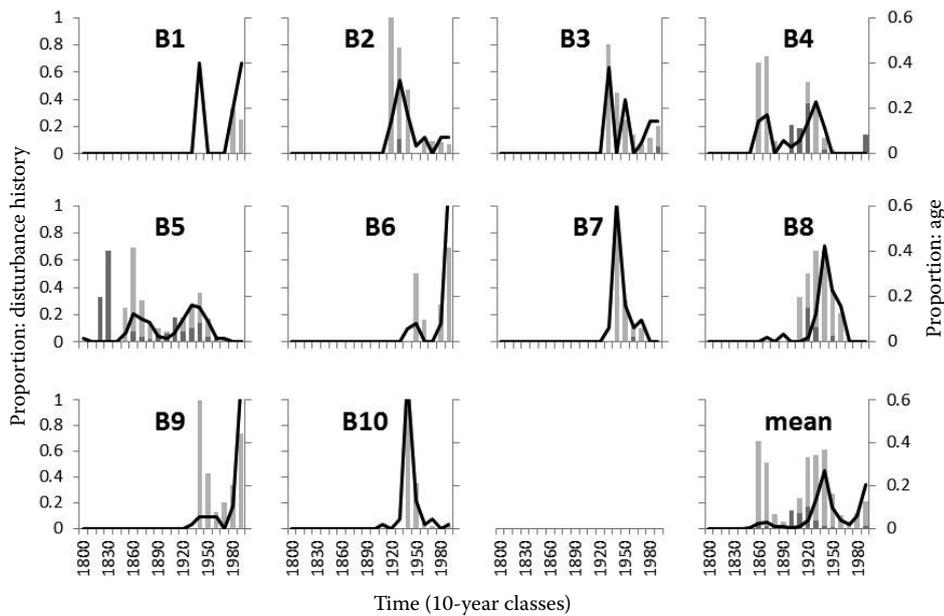
Fig. 2. Age distributions (black lines) and disturbance chronologies (bars). Disturbance chronologies are based on proportions of trees that indicate disturbance either by fast initial growth (light grey bars) or by release from suppression (dark grey bars)

lation. The third wave, which accounts for six percent of the spruce population, recruited between 1860 and 1889. The age class distribution in half of the research plots is represented simply by one cohort with a peak in the 1930s and 1940s. This peak also makes the more pronounced peak on the curves describing the development in plots B4 and B5 where the age class distribution is bimodal. The other peak comes earlier, in the 1860s and 1870s. In plots B6 and B9, the age class distribution resembles an exponential curve with a sharp increase after the year 1980. The oldest individuals can be found in plot B5 and the maximum age is 221 years.

Rapid early growth rate was identified in 86% of the individuals. Releases were observed in 20% of samples. They occurred almost exclusively on the three oldest plots (B4, B5 and B8). The most prominent disturbances were reconstructed into the period 1860–1880 and 1900–1950. The old-

est disturbance period was reconstructed only on the three oldest plots. For other plots, we did not have any sufficient data for the period before 1920. Tree mortality in those periods is supported by the occurrence of releases in 1860–1880 (plot B5) and 1900–1940 (plot B4, B5, B8). The release could be delayed no more than several years after the death of surrounding trees (contrarily to rapid early growth rate). The recruitment of the youngest cohort in the late 20th century is not supported by a sufficient amount of releases, which suggests a lower amount of canopy tree mortality during this period.

Spatial pattern

The spatial autocorrelation of tree canopy accessions was significant mainly in the oldest plots (B4, B5 and B8) with more diverse age distribution (Fig. 3).
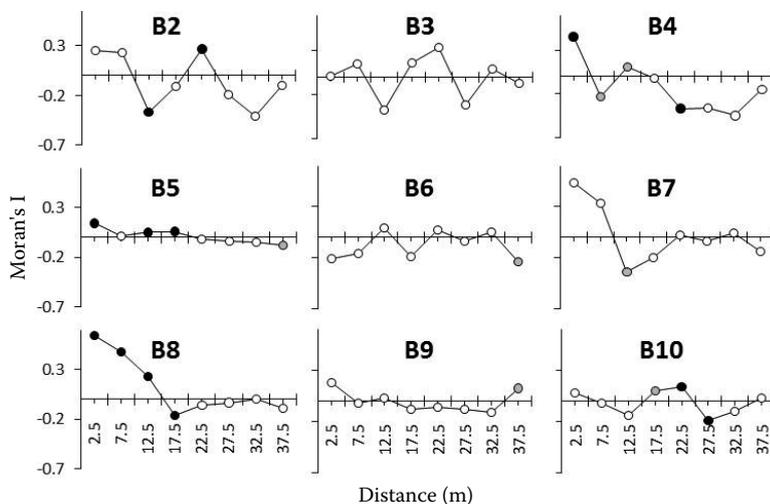
Fig. 3. Moran's correlograms for the age of trees entering the canopy. Values significant at a 5% (and/or 10%) level are represented by black (and/or grey) circles, and non-significant values by white circles. Because of a low number of trees, plot B1 was excluded from the calculations
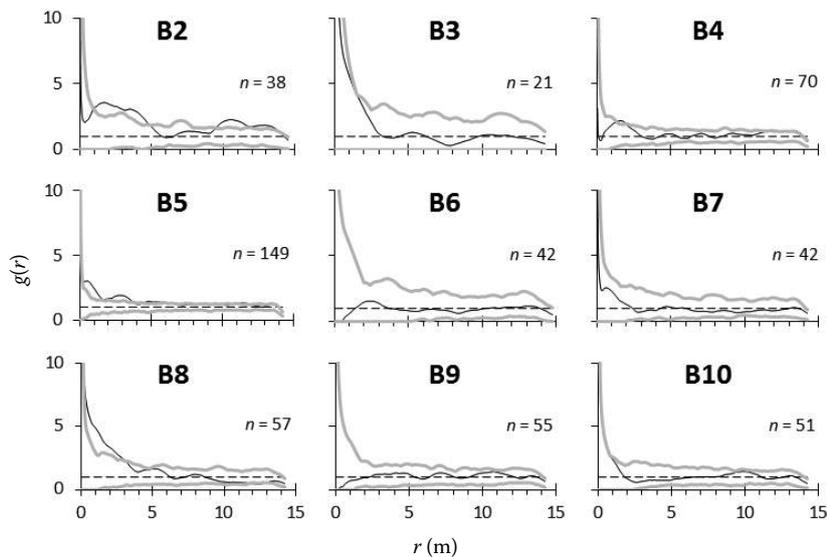
Fig. 4. Pair correlation function $g(r)$ and simulation envelopes for trees (DBH $\geq$ 10 cm) in research plots. Black solid line represents observed value, dashed line theoretical value, and grey lines depict 99% significance interval. n is the number of stems. Values of $g(r)$ outside the simulation envelope indicate significant deviations from random: clustering if above and inhibition if below the envelope

The spatial autocorrelation was demonstrated in those plots mainly on the shortest distance classes from 5 up to 20 m. Other plots did not show a clear spatial autocorrelation of canopy accessions.

The spatial distribution of individuals with DBH $\geq$ 10 cm at distances greater than 5 m was random in all plots (Fig. 4). Trees were distributed in clusters at distances up to 5 m in most plots. In plots B6 and B9 dominated by the youngest cohort, we observed spatial inhibition at distances below 2 meters. Regeneration (individuals with DBH < 10 cm) showed prominent aggregation at short distances (Fig. 5). The analysis revealed a significant cluster distribution at distances from 0 to 2–5 m for most research plots. In plots B2, B4 and B10, clustering occurred also at greater distances – in the range of 6–13 m, 12–14 m and 6.5–8 m respectively. Generally, a significant positive association between trees and regeneration was proved on the shortest distance classes from 0 to 1–3 m (Fig. 6). The spatial asso-

ciation was not different from random in three plots (B3, B6 and B9) and at distances exceeding 3 meters in all plots.

DISCUSSION

According to our results, it is hardly possible to evaluate the extent and severity of the disturbance caused by documented logging in the mid-19th century, owing to a low number of sufficiently old samples in most plots. Only the two most western plots at lower altitudes, on a more waterlogged site, contained a sufficient number of trees older than 1900. Therefore, these plots do not probably represent the whole study area well. For these plots, we reconstructed the disturbance into the period 1860–1880. Since this is based mainly on rapid early growth rates (gap origins), it could be partly explained by a prolonged reac-
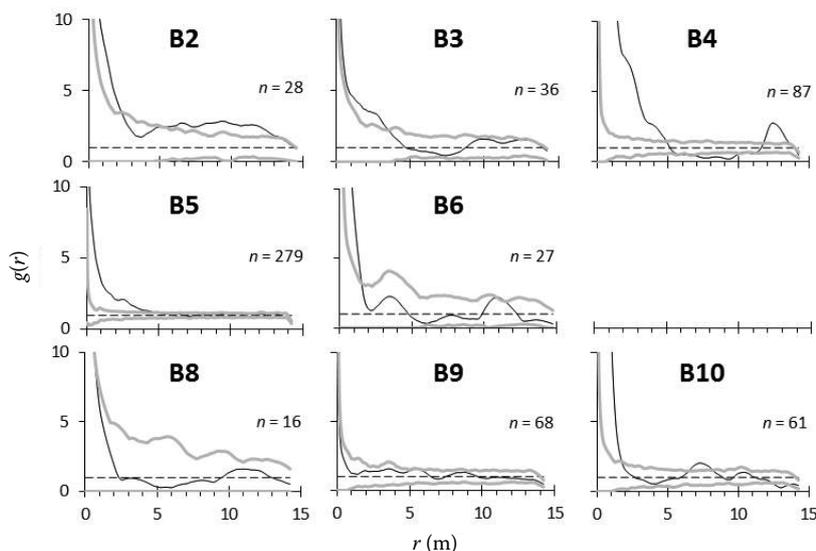
Fig. 5. Pair correlation function $g(r)$ and simulation envelopes for regeneration (DBH < 10 cm) in research plots. Plot B7 together with plot B1 was excluded from calculations because of a low number of recruits. For more details see Fig. 4
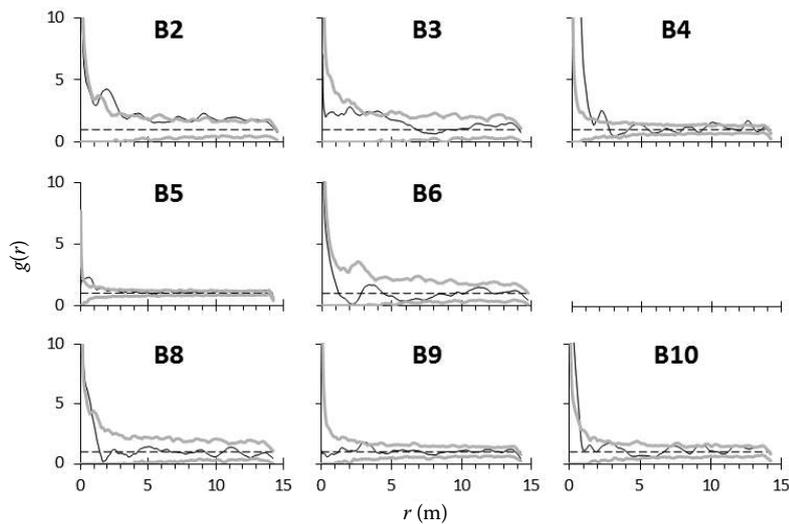
Fig. 6. Cross-type pair correlation function $g_{i,j}(r)$ and simulation envelopes for regeneration and trees in research plots. For more details see Figs 4 and 5

tion to the documented logging in 1846 and 1847 (Vicena 2011). However, several release events in the 1860s and 1870s suggest that the documented windstorms and bark beetle outbreak played an important role on those plots (Ministr 1963; Jelínek 2005). This disturbance did not probably remove all mature trees in these plots and the canopy was not open for a long time because subsequent growth rates of trees were relatively low and many release events occurred later in the early 20th century. We conclude that the documented harvesting in the mid-19th century did not affect the whole study area. It could influence the central part of the stand but our data are not sufficient to test this issue.

The second and dominant cohort was established in the first half of the 20th century. The establishment of this cohort was associated with release events in the three oldest plots. This means that the closed canopy, which was removed by a disturbance, had previously existed at least in those plots. The disturbance chronology and proportion of releases peaked in the 1920s. Disturbance reconstructions for all other plots are based on rapid early growth rates that peaked between 1920s and 1940s. The plots could be affected by similar disturbances like older plots because they were regenerated in the same period as older plots. However, it is also possible that the central part of the study area was free from trees before. The available historical sources do not allow us to fully determine the cases of disturbances in the first half of the 20th century. Nevertheless, they indicate that the area was managed in this period (Klečka 1930). The prolonged period of releases also supports the thesis that there were several individual disturbance events, which could be partly caused by logging operations. On the other hand,

Klečka (1930) also mentioned areas logged after the windthrow in the study area. He claimed that those areas were used for livestock grazing. Several windstorms were documented in the Bohemian Forest in the 1920s, specifically in 1921, 1922 and 1929 (Ministr 1963; Brázdil et al 2004). Likely natural disturbances in old-growth stands which took place in the 1910s and 1920s in the southern part of the Bohemian Forest were reconstructed by Janda (2012) and the disturbances which occurred in the 1920s in several localities across the Bohemian Forest by Čada and Svoboda (2011) and Čada et al. (2013). Thus, we conclude that both natural and anthropogenic disturbances (including logging and livestock grazing) contributed to the establishment of the main cohort in the Jewish Forest in the first half of the 20th century.

The third cohort has been recruiting since the 1980s. The recruitment of this cohort is restricted mainly to the central part of the study area around the mountain top and it is not associated with almost any release events. Therefore, disturbance is not the reason for recruitment of this cohort. The most likely reason is the planting carried out in the study area in the 1970s (Archives of NP Šumava Kašperské Hory, Forest management plan Srní 1969–1978, Javoří Pila forest district). This thesis is supported by the spatial pattern analysis, which shows rather an inhibition of trees below 2 meters and random spatial association between trees and regeneration on plots with the youngest cohort. Trees were probably planted at some distances and gaps were preferred for planting. Until now, not many naturally regenerated trees have likely exceeded the coring limit of 10 cm DBH since 1960.

After the major disturbance in the early 20th century, forest succession went through several

stages of development. In the first stage, the regeneration after the disturbance was relatively fast, comparable to regeneration after a natural disturbance in primary forest (Motta et al. 1999; Svoboda et al. 2010; Panayotov 2011; Čada et al. 2013). The recruitment delay of 1–3 decades could be explained simply by the time which trees need to reach the coring height (Niklasson 2002). After this period the regeneration of new trees was limited, even though the light was not mostly the limiting factor because of low density of the stand. Therefore, we can conclude that the regeneration of the dominant cohort was limited to a short period of suitable conditions after the disturbance. The suitable conditions could have been created by natural disturbance, logging operations and/or cessation of grazing. Enough light, proper microsite availability and no grazing could have facilitated the regeneration (Motta et al. 1999, 2002; Svoboda et al. 2010). On the other hand, the density of the cohort is relatively low, suggesting that the conditions during its establishment were not optimal; human activities likely limited the density and heterogeneity of natural regeneration (Jonášová, Prach 2004; Jonášová, Matějková 2007).

Regeneration is nowadays limited to proper microsites with a low level of competition. In our study area, it means mainly dead wood and places around mature trees. The age structure of mature trees supports the opinion that similar factors were acting during forest succession in the 20th century. Decaying wood is known as a preferred microsite for spruce regeneration (Jonášová, Prach 2004; Kupferschmidt, Bugmann 2005; Ulbrichová et al. 2006; Bače et al. 2009; Jonášová et al. 2010; Svoboda et al. 2010; Čížková el al. 2011) and it appears that it was removed from the stand in the early 20th century. The cover of herb vegetation increases with increasing time since disturbance (Vacek et al. 1999; Kooijman et al. 2000; Fischera et al. 2002; Jonášová, Prach 2004, 2008; Jonášová, Matějková 2007; Vávrová, Cudlín 2010) and, therefore, the competitive demand on tree regeneration also increases. The present herb cover is dominated by *Calamagrostis villosa*, *Deschampsia flexuosa*, *Nardus stricta* and *Vaccinium myrtillus* (Bednařík, Matějka 2011) and is similar to the state described by Klečka (1930) 80 years ago. Many scientific studies state that a plant cover of the mentioned grasses represents a microsite unsuitable for natural regeneration of the Norway spruce (Jonášová, Prach 2004; Kupferschmidt, Bugmann 2005; Holeksa et

al. 2007; Zenáhlíková et al. 2011). We therefore believe that the second cohort was probably established before the expansion of grass turf after the disturbance or after cessation of livestock grazing (Jonášová, Prach 2004; Freléchoux et al. 2007; Janišová et al. 2007; Tasser et al. 2007; Lingua et al. 2008; Pornaro et al. 2013). Today, regeneration is often observed only in areas covered with spruce litter or mosses (Bednařík, Matějka 2014), which are its preferred substrates (Jonášová, Prach 2004; Kupferschmidt, Bugmann 2005; Holeksa et al. 2007; Svoboda, Zenáhlíková 2009; Jonášová et al. 2010). They are usually found under or near large tree crowns where the conditions are not convenient for grass species. This leads to clustering of regeneration at short distances and to the development of a positive relationship between natural regeneration and trees.

Our study found that the succession has not followed the model of gradual colonisation of the area by trees. Instead, it has happened in several different developmental stages. In the first stage, regeneration partly benefited from the available microsite and created sparse canopy. After that, during the second stage, regeneration of new trees has been almost impossible because of microsite limitations. This stage has spanned over several decades until now, when the proper microsite developed on decaying wood and near mature trees. A similar way of facilitation was described in other studies as well (Miller, Halpern 1998; Gömöry at al. 2006; Lingua et al. 2008; Halpern et al. 2010). More than 80 years after the disturbance, trees have not filled all the space yet. They still preserve the clustered spatial pattern created after the disturbance. Creation of clusters is common in formerly grazed stands (Lingua et al. 2008; Halpern et al. 2010; Lamedica et al. 2011) and during stand regeneration. After that, the competition-induced mortality should shift the spatial pattern to random or regular (Zahradník et al. 2010; Lamedica et al. 2011; Janda 2012). This is not the case of the Jewish Forest yet.

CONCLUSIONS

Although different parts of the Jewish Forest are quite similar, their development progressed differently. Waterlogged stands in the area were not probably exposed to strong grazing pressure and regenerated naturally partly after a period of disturbances in the mid-19th century and the con-

tinuity of the forest cover was not interrupted. Open parts near the mountain top were affected by human activities most profoundly. They presumably developed by natural succession after anthropogenic management had ceased. Forest succession in the second half of the 20th century was obstructed by limitation of proper microsite, partly because of the competition from herbs and grasses. Nowadays, about 80 years after the disturbance, proper microsites are developing on decaying wood and near mature trees, allowing the development of new regeneration. The analysis revealed that disturbances caused by human activities, such as livestock grazing and logging, may strongly influence the structure and dynamics of mountain spruce forests. The absence of suitable substrates for natural regeneration can prolong forest succession for many decades. Sparse canopy was formed because of limitations of regeneration due to human activities.

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Corresponding author:

Ing. Jan Bednařík, Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 1176, 165 21 Prague 6-Suchdol, Czech Republic; e-mail: janbednarik@seznam.cz