Forest Ecology and Management 260 (2010) 707–714

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Natural development and regeneration of a Central European montane spruce forest

Miroslav Svoboda[a,*], Shawn Fraver[b], Pavel Janda[a], Radek Bače[a], Jitka Zenáhlíková[a]

[a] Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129, Praha 6 Suchdol 16521, Czech Republic
[b] U.S. Forest Service, Northern Research Station, 1831 Highway 169 East, Grand Rapids, MN 55744, USA

ARTICLE INFO

Article history:
Received 15 March 2010
Received in revised form 12 May 2010
Accepted 17 May 2010

Keywords:
Bark beetle
Competition
Dendrochronology
Dead wood
Stem-mapped plots
Wind disturbance

ABSTRACT

Montane Norway spruce forests of Central Europe have a very long tradition of use for timber production; however, recently there has been increasing concern for their role in maintaining biological diversity. This concern, coupled with recent severe windstorms that led to wide-spread bark beetle outbreaks, has brought the management of montane spruce forests to the forefront of public policy discussions in Central Europe. In order to shed light on the natural development and current structure of mature montane spruce forests, we established four 0.25 ha research plots in a semi-natural montane spruce forest in the Šumava Mountains (The Bohemian Forest), Czech Republic. We mapped all trees, extracted increment cores for age and growth-pattern analyses, and inventoried all current tree regeneration, including the substrates on which it was found. Stands were characterized by uni-modal tree diameter distributions and high basal areas (56.6 m^2 ha^{-1} on average), indicating a natural transition from the stem exclusion phase towards the understory reinitiation phase. The stands showed largely single-cohort recruitment age structures, however, with recruitment spanning seven decades. Our analyses suggest that this cohort existed as advance regeneration prior to major disturbances in the late 1800s, which included post-bark beetle salvage logging. Spatial pattern analyses of living and dead stems combined, showed an increase in uniformity of living trees, pointing to the role of natural density-dependent mortality. However, past growth patterns and historical documentation suggest that low intensity canopy disturbances (wind and snow) also caused mortality and diversified canopy structure. Because the stands developed naturally over the past 120+ years and thus escaped thinning operations, high volumes of coarse woody debris (94 m^3 ha^{-1}) and snag densities (546 stems ha^{-1}) have accrued. Advance spruce regeneration was quite abundant and existed primarily on deadwood substrates, even though these occupied only a small percent of stand area. Because of salvage logging in the late 1880s, these stands do not qualify, according to the traditional paradigm, as natural spruce forests. As a result, they are recently subject to active management practices including salvage logging that remove dead and dying trees. Given the importance of deadwood for forest regeneration and recovery from disturbance, as demonstrated in this study, we argue that dead wood removal may limit future natural regeneration in these stands. Thus, the purported benefits of removing dead and dying trees from semi-natural forests must be carefully weighed against the potential detrimental impacts on natural spruce forest regeneration and biodiversity.

1. Introduction

Forests dominated by Norway spruce (*Picea abies*) cover a significant area of Central Europe's mountainous region. These forests have a very long history of human use, including timber production and the protection of human populations and infrastructures from avalanches and flooding (Kräuchi et al., 2000; Brang, 2001; Spiecker, 2003). Recent concerns, however, have shifted forest management objectives to address biodiversity conservation (Kräuchi et al., 2000). As a result, two national parks have recently been created – one in the Czech Republic (Šumava National Park), the other in Germany (Bayerischer Wald National Park) – to protect montane spruce forests. Together, these two adjacent parks cover more than 100 000 ha of forested landscape. The formation of these parks has raised many scientific and practical questions regarding forest management and conservation practices in this region (Jonášová and Prach, 2004, 2008; Jonášová and Matějková, 2007; Müller et al., 2008; Hais et al., 2009).

---

* Corresponding author at: Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Department of Silviculture, Kamýcká 129, Praha 6 Suchdol 16521, Czech Republic. Tel.: +420 224 383 405; fax: +420 234 381 860.
E-mail addresses: svobodam@fld.czu.cz (M. Svoboda), sfraver@fs.fed.us (S. Fraver), janda@fld.czu.cz (P. Janda), bace@fld.czu.cz (R. Bače), zenahlikova@fld.czu.cz (J. Zenáhlíková).

0378-1127/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2010.05.027

One prerequisite for the proper management of montane spruce forests is an understanding of their natural disturbance dynamics at both the stand and landscape level (Kuuluvainen, 2002; Lindenmayer et al., 2006). Such information provides the foundation on which sustainable forestry practices can be developed (Bergeron and Harvey, 1997; Seymour and Hunter, 1999). Management practices developed in the absence of such information may be unnecessarily controversial, inefficient, or counterproductive.

A number of studies from Central Europe have addressed natural dynamics of mixed mountain beech-fir forests (e.g., Nagel et al., 2006; Nagel and Svoboda, 2008; Šamonil et al., 2009). Yet few studies in this region have addressed natural dynamics of subalpine or montane Norway spruce forests (Motta et al., 1999; Holeksa et al., 2007; Zielonka et al., 2010). To date, most of the studies on the natural dynamics of Norway spruce forests have come from Fenno-Scandinavia (Hofgaard, 1993; Kuuluvainen et al., 1998; Wallenius et al., 2005; Fraver et al., 2008). Such studies are scarce in Central Europe because (1) large areas of unmanaged spruce forests in which to evaluate natural disturbances are quite rare, and (2) the long history of human land use makes it difficult to disentangle natural from anthropogenic influences (Motta et al., 2002). Given the differences in climate and primary disturbance agents, it is unlikely that inferences drawn from studies outside this region apply to forests of Central Europe. For example, the research focus on large wildfires in Fenno-Scandinavian spruce systems (e.g., Engelmark et al., 1994) has little relevance to Central Europe. Here, convective windstorms and spruce bark beetle (*Ips typographus*) outbreaks represent the potential large-scale disturbances (Dobrovolný and Brázdil, 2003; Wermelinger, 2004). Historically, these disturbances have received little research attention, in part because they were thought to play a minor role in forest dynamics and biodiversity (Korpel, 1995; Leibundgut, 1987), and in part because the amount of damage they caused was thought be the result of previous forest management practices. However, a recent chain of events – severe windstorms in 1986, 1999, 2007, and 2008 that caused widespread forest damage leading to extensive bark beetle outbreaks – has called attention to such disturbances, suggesting their role may be greater than had been previously thought. These events have brought the management of montane spruce forests, particularly the practice of salvage logging, to the forefront of public policy discussions in Central Europe.

Thus, the general objective of this study was to reconstruct the disturbance history and development of a semi-natural montane Norway spruce forest in order to determine how these events have shaped its current structure and composition. The study site, located in the Šumava Mountains of the Czech Republic, represents the largest and best preserved natural (origin and development without human intervention) and semi-natural (minimal human intervention) spruce forests in the country. A previous study concluded that the forest structure differed throughout an old-growth portion of this site, probably as a result of the past disturbances and changing site conditions (Svoboda and Pouska, 2008). In this current study we examine an additional portion of this site that possesses a number of features characteristic of mature semi-natural forest, despite the known history of disturbance and salvage logging, which took place 130–140 years ago. In central Europe, where true old-growth forests (forests that have escaped harvest and reached an advanced stage of development) are quite rare, information on regeneration, stand development, and stand structure from such semi-natural forests is the best alternative for informing management decisions intended to emulate natural processes (Kulakowski and Bebi, 2004; Motta and Edouard, 2005). Our specific objectives were to (1) determine the stand origin and disturbance history of this site using historical documents and methods of dendrochronology, (2) assess the role of density-dependent mortality in shaping current forest structure using spatial pattern analyses, and (3) evaluate seedling substrate preferences to further elucidate stand origin and development. Results from this study can inform management decisions in light of the recent establishment of national parks and subsequent major disturbances.

2. Methods

2.1. Study area and land-use history

This study was conducted in Šumava National Park (the Bohemian Forest), southern Czech Republic. The study area is immediately adjacent to a 600-ha tract of what is considered the best example of an old-growth spruce forest in the Czech Republic. The area lies on a gentle north-facing slope (elevation about 1100–1200 m) below the old-growth site on the ridge between Třístoličník and Trojmezná (48°47′N, 13°49′E). The mean annual precipitation at this altitude is about 1200–1400 mm, and the mean annual temperature is about 4 °C (Svoboda et al., 2006b). The soil substrate in this area consists of Lithic Leptosols, Hyperskeletic Leptosols (Humic and Dystric), and Dystric Cambisols. These soils are derived from biotitic coarse grained granite. The forest is dominated by Norway spruce (*P. abies*), with rowan (*Sorbus aucuparia*) forming a minor component (Svoboda et al., 2006a; Svoboda, 2007; Svoboda and Zenáhlíková, 2009). The Bohemian Forest was in the past affected by acid deposition and has been recovering during last decade (Šantrůčková et al., 2007).

We selected the study area in part by using historical forestry management plans that contained age structures, species composition, logging intensity, and areas disturbed by wind, bark beetle and salvage logging, with data extending back to 1856 (Jelínek, 2005). These plans were digitized and linked with aerial photos (historical and recent), and recent forestry plans in a GIS. Based on these GIS overlays, we selected an area of about 300 ha that had been classified as old-growth forest before 1868. Documented windstorms in 1868 and 1870 led to wide-spread outbreaks of the spruce bark beetle in this area, which began around 1869 and persisted at least through 1880–1890 (Jelínek, 2005). The salvage logging that followed transformed the area into a young post-disturbance stand. Maps from 1902 show the area to be in the 0–20 year age class (Jelínek, 2005). There were no records of tree planting in management plans.

The forest developed naturally (i.e., without human intervention) in subsequent decades. Canopy disturbances from snow and wind damage between 1922 and 1933 (Jelínek, 2005) caused patchy tree mortality, which no doubt affected competitive interactions and growth rates in surviving trees. As of 1948 the study area formed part of the large no-entry military zone, and no major management measures were undertaken until 1989 when the military zone was abolished. In 1991, Šumava National Park was established, and the study area became part of the park's core protected zone. However, patchy wind damage and bark beetle outbreaks in the early 1990s created controversy regarding management, and the area was ultimately withdrawn from the core zone in 1995, at which time about half of the area was salvage logged.

2.2. Data collection

Four 0.25 ha (50 m × 50 m) permanent sampling plots (plots A–D) were established in the study area in 2006 and 2007. Plot locations were selected according to the following constraints: (1) plots must be centered within the larger remnants of closed-canopy forest to avoid edge effects; (2) plots must be dispersed as regularly as possible across the study area; (3) plots could not include anomalous site conditions such as stream corridors, rock outcrops, or evidence of recent salvage logging.

Electronic and laser measuring devices linked to a GIS (Field-Map®, Monitoring and Mapping Solutions, Ltd.; www.fieldmap.cz) were used to establish the plots, map all trees and down woody debris (DWD), map and measure tree crown projection areas, and establish a grid for regeneration surveys. The areas of individual tree crowns were summed in a GIS to calculate the percent canopy openness for each plot. For each tree ≥5 cm diameter at breast height (1.3 m, DBH), we recorded DBH and height; for each stump (≤1.3 m height, ≥10 cm basal diameter), we recorded top diameter; and for each piece of DWD ≥10 cm diameter and ≥2 m length, we recorded large and small end diameters, length, and decay class (using a five-class system as per Maser et al., 1979). The volume of each DWD piece was calculated using the conic-paraboloid formula, which has greater accuracy than traditional formulae (Fraver et al., 2007). Volumes of pieces in decay classes IV and V were multiplied by cross-sectional height–width ratios (0.86 and 0.50, respectively) to adjust for collapse during decay (ratios determined from decayed Norway spruce in Sweden, *unpublished data*).

To analyze tree age structure and radial growth patterns, we divided the plot into twenty five 10-by-10 m cells and extracted one increment core at breast height from the canopy tree nearest the cell center. We then conducted a complete inventory of tree regeneration by dividing each plot into hundred 5-by-5 m cells. Within each cell, we recorded the number and heights (in 10-cm classes) of spruce and rowan saplings >20 cm height, but less than 5 cm DBH. We also recorded the substrates occupied by each, using the following four categories: down logs, tree stumps, leaf litter and vegetation. Spruce and rowan seedlings <20 cm were surveyed in this same way, but only in the central 16 cells in each plot.

2.3. Data analysis

2.3.1. Stand origin and disturbance history

Increment cores were attached to wooden mounts and shaved with a scalpel before analyses. The cores were visually cross-dated by identifying narrow marker years (Yamaguchi, 1991). Ring widths were measured to the nearest 0.01 mm using a stereomicroscope and a Time-Table sliding-stage measuring device in conjunction with PAST32 software. Following measurement, cross-dating was verified with COFECHA software (Holmes, 1983). For cores that missed the pith, we used Duncan's (1989) method to estimate the number of years missed, based on the mean growth rate of the innermost five complete rings. Because Norway spruce seedlings can become established and persist for decades under shade, we consider an individual to be recruited into the stand only when it surpasses breast height. Thus no attempt was made to estimate tree ages since germination; we simply refer to the number of annual rings at breast height as the recruitment age (we return to this topic in Section 4).

We evaluated each tree-ring series (i.e., growth pattern derived form each core) for evidence of rapid early growth, as such evidence indicates the tree experienced open, free-to-grow conditions at the time it reached breast height (Lorimer and Frelich, 1989). Trees were considered to be open-recruited if the mean ring width for the first 5 years in the series exceeded 1.93 mm (determined by binary logistic regression of sapling growth in open and closed-canopy positions, Janda et al., in press), and the subsequent growth pattern was declining, parabolic, or flat (Frelich, 2002).

To further shed light on stand development, we produced standardized growth chronologies, using all properly dated cores, to evaluate stand-level growth patterns through development. We separated the data into two groups: trees forming members of a large cohort established in the 1890s, and those that existed, presumably as advance regeneration, prior to that large cohort. The chronologies were developed using the ARSTAN program (Cook and Krusic, 2005) by first fitting a horizontal line through the mean ring width for each tree-ring series, then dividing ring widths by the fitted values, resulting in a unit-less index for each year in the series (Fritts, 1978). Individual indexed series were then averaged to produce the two standardized chronologies. Using the horizontal line, as opposed to a curve-fitting technique, does not detrend the series, and thus maintains low- to medium-frequency growth trends, assumed to be largely the result of disturbance (Veblen et al., 1991).

2.3.2. The role of density-dependent mortality

We used spatial pattern analyses of living and dead trees to shed light on the role of density-dependent mortality in past stand development. First, we tested for a shift from aggregation toward uniformity through stand development, which would suggest density-dependent thinning from competition (Kenkel, 1988). Second, we tested if the pattern of living trees was more uniform than that of the living and dead trees combined, also implicating competition as a driving factor (Duncan, 1991; Shackleton, 2002).

A pair-correlation function (Wiegand and Moloney, 2004) was used for analysis of the spatial patterning. This function is analogous of the widely used Ripley's $K(r)$ function (Ripley, 1981; Diggle, 1983), but is considered to be more powerful at detecting spatial patterns across scales (Wiegand and Moloney, 2004). Approximate 95% confidence envelopes were determined using the 5th lowest and 5th highest value of 99 Monte Carlo simulations under the complete spatial randomness null model. Note that this is not a goodness-of-fit test with exact confidence intervals (Loosmore and Ford, 2006; Getzin and Wiegand, 2007). All analyses were performed using the Programita software (Wiegand and Moloney, 2004).

To address the first question, we assessed the spatial pattern of live and dead trees (pre-mortality pattern), testing against a heterogeneous Poisson process. A heterogeneous Poisson process was chosen because our plots were influenced by first-order heterogeneity (Fig. 1). Using methods proposed by Wiegand and Moloney (2004), a circular moving window with a fixed radius R was used to estimate intensity (i.e., mean number of events per unit area). Therefore, our results may be interpreted only up to a radius of $R = 10$ m.

To address the second question, we compared the spatial pattern of live trees (post-mortality pattern) to that of live and dead trees combined. We reasoned that a shift from a random distribution of live and dead trees (reflecting the pattern of early tree establishment) to a uniform distribution of live (i.e., surviving) trees would suggest density-dependent mortality from competition. We then determined if the live trees formed a uniform spatial distribution using univariate random labeling as the null model (Wiegand and Moloney, 2004). Specifically, this test assesses whether the surviving trees are a random subset of the joined (live and dead spatial) pattern. This was accomplished by computing the function $g(r)$ from the observed data, then randomly re-sampling sets of dead trees from the joined pattern and generating the appropriate confidence limits. A similar approach was used by Getzin et al. (2006).

2.3.3. Tree regeneration and substrate preferences

We used the χ^2 statistic to test the null hypothesis that tree regeneration density was independent of substrate type. The area occupied by litter and vegetation substrates (i.e., microsites) was visually estimated in each 5-by-5 m cell. For down-log and tree-stump substrates, the area was calculated as a trapezoid (logs) or a circle (stumps) projected onto the ground. Data were pooled from all cells and plots for analysis.

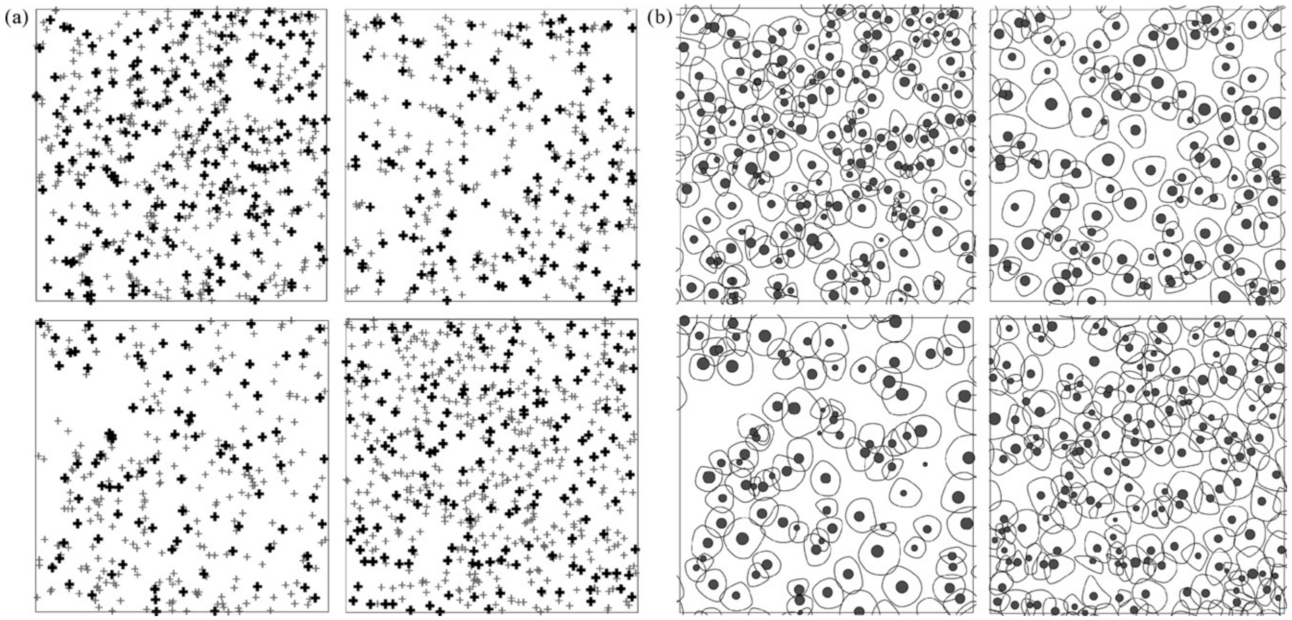

Fig. 1. (a) Stem maps of living (bold dark cross) and dead (grey cross) trees, showing a general trend toward spatial uniformity in living trees when compared the combined pattern of living and dead trees, suggesting density-dependent mortality. (b) Maps of living trees and crown projection areas (dot size proportional to tree diameter), showing considerable canopy patchiness, even though these sites have not reached the old-growth stage. In both panels, Plots A and B are in the upper left and right, and Plots C and D are in the lower left and right.

Table 1
Structural characteristics of the study plots. BA = basal area (m^2 ha^{-1}); DWD = down woody debris; seedlings are tree stems <20 cm height; saplings are ≥20 cm height.

	Live trees		Snags		Saplings	Seedlings	DWD vol.	% Canopy
	BA ha^{-1}	Stems ha^{-1}	BA ha^{-1}	Stems ha^{-1}	Stems ha^{-1}	Stems ha^{-1}	m^3 ha^{-1}	Openness
Plot A	63.8	732	19.2	868	3600	52,225	51.3	30.7
Plot B	60.2	480	20.7	548	5664	35,325	61.8	36.6
Plot C	49.3	364	10.5	276	13,404	20,650	123.6	41.6
Plot D	52.6	628	11.8	492	24,560	62,925	141.0	19.0
Mean	56.5	551	15.6	546	11,807	42,781	94.4	32.0

3. Results

3.1. Stand structure

Norway spruce accounted for nearly 100% of basal area, with rowan the remainder. Data pooled across plots revealed a mean live-tree basal area of 56.5 m^2 ha^{-1} and density of 551 trees ha^{-1}, with snag basal area at 15.6 m^2 ha^{-1} and density of 546 snags ha^{-1}. The mean seedling density was 42 781 ha^{-1}, of which 100% were Norway spruce. The mean sapling density was 11 807 ha^{-1} of which 91% were Norway spruce, the remainder being rowan. The mean DWD volume was 94.4 m^3 ha^{-1}, after adjusting for collapse of advanced decayed pieces (see Section 2.2). Though the current vertical canopy structure is rather homogenous within a site (i.e., canopies occurring in one strata), the horizontal canopy structure is quite patchy, as shown in Fig. 1. In addition to this within-site patchiness, canopy openness varied quite a bit from plot to plot, with a mean of 32% openness (SD = 9.7). Coarse woody debris existed across the range of decay classes; however, it had highest abundance and volume in classes III and IV (sites pooled). Table 1 provides additional plot-level structural data. Both living and dead spruce trees showed unimodal bell-shaped diameter distributions (Fig. 2, sites pooled), with the peak in dead-stem diameters about 15–25 cm, and the peak for the live stems about 30–40 cm.

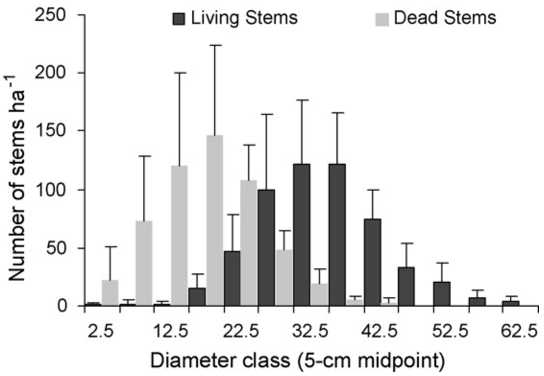

Fig. 2. Diameter distribution of the living and dead trees (plots pooled) showing the living trees to be larger than the dead trees, suggesting competition as the mortality agent as stands developed through the stem exclusion stage. Errors bars represent standard deviations.

3.2. Stand origin and disturbance history

Age structures clearly show a major cohort being recruited in the 1890s and the two decades that followed (Fig. 3). However, numerous trees had become recruited in the decades prior to 1890, resulting in a prolonged recruitment period spanning seven decades (Fig. 3). Analyses of growth patterns suggest open conditions during four of these early decades, as sizeable percentages of trees recruited in the 1870s, and 1890s through 1910s met the radial-growth criteria for open-grown conditions (Fig. 3). Further,

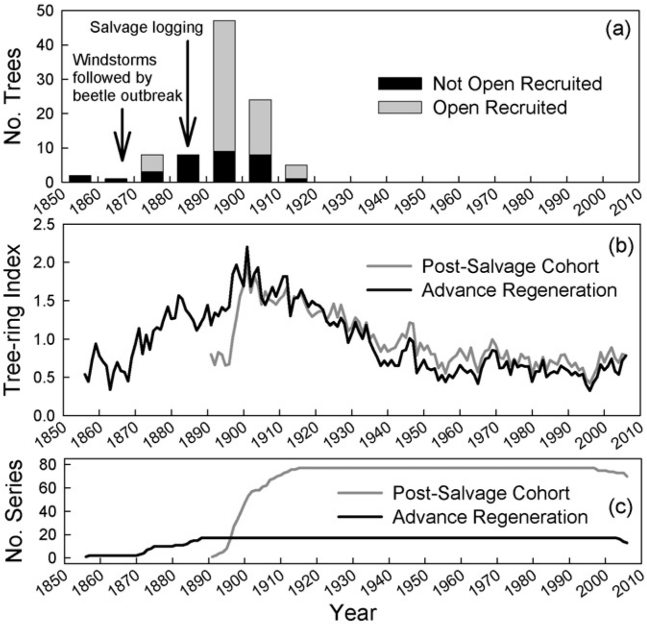

Fig. 3. (a) Recruitment age structures as they relate to historically documented disturbances (shown by arrows). Open vs. not-open recruitments were based on early growth rates (see text). (b) Standardized radial-growth trends of the earliest advance regeneration and the post-salvage logging cohort, showing growth increases (advance regeneration) or rapid early growth (post-salvage cohort) in response to these known disturbances. The variability of growth during the 1900s is the result of documented low-severity wind and snow disturbances. (c) Sample size (number of tree-ring series) on which the standardized growth chronologies were derived.

standardized growth chronologies reveal rapid early growth in trees comprising the major cohort beginning in the 1890s, and consistently increasing growth in trees recruited prior to 1890 (Fig. 3). Radial growth culminates around 1900 and declines somewhat steadily through stand development.

3.3. The role of density-dependent mortality

Specific results of the spatial pattern analyses (Table 2) varied somewhat among plots. In the case of the spatial pattern of live and dead trees (pre-mortality pattern), plot A showed that the pattern was uniform from 2.0 to 2.5 m, followed by a tendency towards uniformity from 3.5 up to 4.5 m. Plot B showed this pattern to be clumped from 0.5 to 1 m, followed by a tendency towards uniformity at 4 and 5.5 m. Plot D showed this pattern to be uniform from 0.5 up to 1.5 m. In contrast, Plot C clearly showed spatial randomness at all scales for the combined living and dead trees. In the case of the spatial pattern of living spruce trees (post-mortality pattern), there was a tendency toward more uniform patterning from 0.5 m up to 3 m in all plots. Evidence was strongest on the Plots A, B and D and weakest and Plot C, which is consistent with the random pattern of living and dead trees found there.

3.4. Tree regeneration and substrate preferences

The density of advance regeneration was rather high, with mean seedling density at 42 781 stems ha^{-1} and mean sapling density at 11 807 stems ha^{-1} (Table 1). Densities significantly decreased with the increasing height of individuals (data not shown), suggesting higher mortality for large, presumably older, saplings. Results of the χ^2 test revealed significantly higher observed densities of spruce saplings compared to expected densities on the logs and stump substrates, while lower observed densities were found on other substrates. From 35 to 75% and from 50 to 80% of spruce seedlings and saplings, respectively, were growing on dead wood substrates (logs and stumps), even though these substrate types covered only 4–9% of plots area. Spruce seedlings were aggregated in space as a probable result of this pattern (not shown).

4. Discussion

4.1. Stand origin, disturbance history and stand development

The question concerning stand origin was only partially answered owing to a low number of samples representing the period prior to 1900. Nevertheless, our results show that a number of individuals existed at breast height before the windstorms of 1868 and 1870 and the bark beetle outbreak that immediately followed. Here it is important to note that Fig. 3 shows recruitment ages (i.e., at breast height); actual ages (i.e., since germination) would provide even stronger evidence of the presence of advance regeneration at the time of these disturbances. For example, whorl counts of about 40 current saplings from these same plots suggest and average age of 25 years to achieve breast height. If we assume the advance regeneration in the late 1800s grew at a similar rate, we reason that most of the currently living trees existed as advance regeneration at the time of the disturbances in the late 1800s. This natural advance regeneration responded to these canopy removals with increased growth relative to that of the presumably closed-canopy forest prior to these disturbances (Fig. 3). This response is even more pronounced during the salvage logging that likely began in the 1870s and continued till 1890s (Fig. 3). The large cohort originating around 1900 likely also consisted of advance regeneration, as well as seedlings established shortly after the windthrow. The successful establishment of this cohort was likely made possible by the combination of relatively open canopy conditions and abundant suitable substrates (addressed below). This interpretation is consistent with the well-known importance of advance regeneration in spruce forests throughout the northern hemi-

Table 2
Results of the spatial pattern analysis of the living and dead tree (pre-mortality pattern) in upper part of the table, and living trees (post-mortality pattern). Results of the pair-correlation function are interpreted only up to 10 m, due to used method of analysis (see methodology). The letters in the table express: c – clumped, r – random, and u – uniform. There is a general trend toward spatial uniformity in living trees when compared the combined pattern of living and dead trees.

	Plot	Distance (m)																			
		0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0
Live and dead stems together (pre-mortality pattern)	A	r	r	r	r	u	r	r	u	u	r	r	r	r	r	r	r	r	r	r	r
	B	r	c	r	r	r	r	r	u	r	r	u	r	r	r	r	r	c	r	u	r
	C	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
	D	r	u	u	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
Live stems (post-mortality pattern)	A	r	u	u	u	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
	B	r	u	u	u	u	r	r	r	c	r	r	r	r	r	r	r	r	u	r	r
	C	r	r	r	r	r	u	r	r	r	r	r	r	r	r	r	r	r	r	r	r
	D	r	u	u	r	r	u	r	r	r	r	r	u	r	r	r	r	r	r	c	r

sphere (Hofgaard, 1993; Kuuluvainen, 1994; Fraver and White, 2005). The combination of these successive events – establishment of advance regeneration, windstorm, bark beetle outbreak, and salvage logging, all occurring during early stand development – explains the prolonged recruitment period, which spans seven decades.

Several lines of evidence reveal that this forest has undergone natural developmental processes following its initiation in the late 1800s. The relatively high density and basal area of living trees ($56.5\,\mathrm{m}^2$ and $551\,\mathrm{trees\,ha}^{-1}$), the high density of dead trees ($546\,\mathrm{snags\,ha}^{-1}$), coupled with the unimodal diameter distributions depict a mature stand in transition from stem exclusion to understory re-initiation development stages (Oliver and Larson, 1996). The declining stand-level growth pattern, following an initial period of rapid growth, is also indicative of this stage of stand development (Veblen et al., 1991), as is the relatively uniform, single-strata canopy structure. This uniformity existed despite the prolonged recruitment period (spanning seven decades), which is consistent with Korpel's (1995) finding that Central European spruce forests in favorable site conditions develop more or less homogenous closed canopies, even if within-stand age diversity reaches 100 years or more.

Competitive interactions, in part mediated by low-severity canopy disturbances, have also played an important role in the natural development of this forest. The post-mortality spatial pattern of living spruce stems, compared to the pre-mortality pattern of living and dead trees, was more uniform in three of the four plots, which suggests density-dependent mortality as a result of competition for resources (He and Duncan, 2000; Shackleton, 2002; Castagneri et al., 2010). Perhaps not coincidentally, the plot on which this general pattern was not seen (Plot C) had the highest percent canopy openness and correspondingly lowest density of living trees, suggesting that canopy disturbances have played a larger role, thereby disrupting the spatial pattern that would have developed primarily from competition. The sheer number of snags seen on all plots (exceeding that of trees) further attests to the strong influence of past competition in this forest. Canopy disturbances, however, alter these competitive interactions by selectively removing trees, thereby increasing resource availability to surviving neighbors. Documented canopy disturbances from snow and wind in the 1920s (Jelínek, 2005) can explain the stand-level variability in growth during that time (Fig. 1), and such disturbances likely explain further variability in the 1940s and 1960s. Additional evidence for such disturbances were seen as abrupt and sustained increases in growth (i.e., growth releases) on a number of individual trees during these decades (data not shown). Finally, the high growth variability seen in the 1990s is attributed to documented wind storms at that time (Fig. 3). The patchiness in canopy structure caused by these disturbances can be seen in maps of canopy projections for each plot (Fig. 1). Thus both competition and low-severity disturbance by wind and snow influence growth rates and mortality, and they contribute to horizontal structural diversity at the stand level.

However, competition and low-severity disturbances alter stand structure in quite different ways. In this case of competition, smaller stems are more likely to die because of poor resource acquisition (Kozlowski et al., 1991; Oliver and Larson, 1996). This result was borne out in the diameter distributions of living and dead trees: although both had uni-modal distributions, the peak in the dead-tree distribution was about 40 cm lower than that of the living trees. In the case of disturbances, larger trees with exposed crowns are more likely to be killed by wind or snow loads (Brokaw et al., 2004; Canham et al., 2001). Indeed, in these stands we observed numerous large trees with damaged crowns and broken tops.

By affecting larger and smaller trees differently, competition and wind disturbance, in combination, create an abundance and diversity of deadwood sizes. The volumes of coarse woody debris reported here fall within the natural range of variability for true old-growth spruce forests from throughout the northern hemisphere (e.g., Kuuluvainen et al., 1998; Jonsson, 2000; Siitonen et al., 2000; Fraver and White, 2005). The snag volumes reported here are unusually high, even for old-growth, owing to the transition from stem exclusion to understory re-initiation.

4.2. Tree regeneration and substrate preferences

The current abundance of spruce seedlings and saplings was strongly and positively linked to the presence of coarse woody debris. Even though coarse woody debris substrates occupied only several percent of the total plot area, the proportion of spruce saplings growing on such sites ranged from 50 to 80%. The importance of these fallen logs and decayed stumps as 'nurse logs' for spruce regeneration has been well recognized in Central Europe (Hunziker and Brang, 2005; Motta et al., 2006; Zielonka, 2006; Baier et al., 2007; Bače et al., 2009). Because of this strong link between spruce regeneration and coarse woody debris, the pattern of regeneration was not spatially random and varied according to substrate. In particular, regeneration often formed strikingly linear patterns (not shown), reflecting the presence of fallen logs. This linearity can also be seen in the current tree strata, at times in conjunction with stilt roots, both reflecting the existence of former suitable nurse logs, which would have been present during stand establishment in the late 1800s.

The extremely high density of advance regeneration (Table 1) is attributable to a combination of abundant suitably decayed nurse logs and the presence of small canopy openings, which have led to current canopy openness ranging from about 19–42% among plots, as well as considerable patchiness in canopy cover (Fig. 1). Contrary to our results, relatively lower densities of advance spruce regeneration have been reported in montane forests in this same geographical region (Jonášová and Prach, 2004; Kupferschmid et al., 2006; Rammig et al., 2007; Heurich, 2009). However, in contrast to our study, most sites included in these studies had been repeatedly thinned to control bark beetle outbreaks as well as other pests, which removed the source of dead and dying trees that ultimately become suitable nurse logs. Thus, our results highlight the importance of coarse woody debris, as well as partial canopy openings, for the regeneration of spruce in these forests.

5. Conclusions and implications for forest management

Results from this mature, semi-natural montane spruce forest show that, in the absence of human intervention, natural processes such as density-dependent mortality and low-severity canopy disturbances have created ample deadwood, both as snags and down woody debris, even though this forest has currently not reached the old-growth stage where such structures might be expected. These processes have also created considerable horizontal patchiness, further adding to the overall structural heterogeneity of the site. The high coarse woody debris volumes, which lie within the natural range of variability of true old-growth spruce forests (above), as well as the occurrence of coarse woody debris in various sizes and states of decay, also highlight the conservation value of these stands for maintaining deadwood-dependent organisms (Martikainen et al., 1999; Siitonen, 2001; Kuuluvainen et al., 2002; Penttila et al., 2004; Pouska et al., 2010). Our results also show that these abundant downed logs serve as the primary substrates for successful spruce seedling establishment. The ability of this forest to accrue advance regeneration, even at the end of the stem exclusion stage, is critical for forest recovery following future disturbances, such as windthrow or bark beetle outbreak.

In Central Europe, removing dead, dying or damaged trees during thinning or salvage operations is a common practice in montane spruce stands. The practice is justified on the grounds that it will reduce their susceptibility to attack by various pests or their vulnerability to damage once attacked (Wermelinger, 2004). Repeated entries of these types have led to dramatic reductions in coarse woody debris abundance in central Europe (Bütler et al., 2004; Lachat and Bütler, 2009). As a result, the quality and quantity of nurse logs suitable for spruce regeneration is correspondingly low, which dramatically reduces the density of advance regeneration. Recent concerns over the failure of natural spruce recruitment following stand-replacing disturbances in Central Europe (Kupferschmid et al., 2006; Rammig et al., 2007) might be most easily attributed to the absence of nurse logs owing to these past management practices. Because dead wood requires several decades to decay to the point of providing suitable seedbeds (Zielonka, 2006), these practices compromise spruce regeneration for decades beyond their initial occurrence. Without dead wood to support spruce regeneration, we must rely on artificial regeneration (i.e., planting), which is especially expensive and laborious in mountain regions, and may not be feasible over large areas. Thus, the purported benefits of removing dead and dying trees from semi-natural forests must be carefully weighed against the potential detrimental impacts on natural spruce forest regeneration and biodiversity.

Because of salvage logging in the late 1800s the fairly homogenous vertical canopy structure, these stands do not qualify – according to the traditional paradigm – as natural spruce forests (Korpel, 1995). By not qualifying, they are thought to have limited conservation value, and are thus subject to active management practices, including salvage logging. However, recent studies suggest that this paradigm should be at least partly reconsidered (Kulakowski and Bebi, 2004; Holeksa et al., 2007; Svoboda and Pouska, 2008; Zielonka et al., 2010), because semi-natural stands may also contain significant structural elements that support biodiversity. Infrequent moderate- to high-severity disturbances such as windstorms and bark beetle outbreaks in semi-natural forests may diversify these stands, thereby enhancing these structures (Müller et al., 2008). The stands and stand structures evaluated in the current study are ideal examples of semi-natural forests that developed following this type of high-severity disturbance. In fact, Svoboda and Wild (2007) showed that in the Bohemian Forest region several thousand hectares of forests similar to the one evaluated here may exist.

The conservation value of semi-natural, maturing spruce forests has been documented elsewhere in northern Europe. For example, both Storaunet et al. (2000) and Jönsson et al. (2009) found that spruce forests 100–150 years post-disturbance (i.e., comparable in age to stands in the current study) contained many, but not all, the important structures of true old growth. This fact forms the basis of the *woodland key habitat* programs of Nordic and Baltic countries, in which areas are voluntarily set aside, regardless of their management histories, because they support structures and species important for biodiversity protection. Adopting such a view in Central Europe may be timely given the demonstrated structural attributes of semi-natural stands, as well as the scarcity of true old-growth forests in this region.

Acknowledgements

This study was supported by the Czech Science Foundation, project no. P504/10/1644 and project no. P504/10/0843. We would like to thank A. Husník, K. Nechuta, L. Bílek, and Š. Hofmeister for assistance in the field. We are especially grateful to J. Wild, M. Jonášová, M. Kopecký, T. Nagel, D. Hardekopf, and K. Edwards for providing valuable comments on earlier drafts of the manuscript. Comments by anonymous reviewers have greatly improved the manuscript. We thank the Šumava National Park authorities for administrative support.

References

Bače, R., Janda, P., Svoboda, M., 2009. Vliv mikrostanoviště a horního stromového patra na stav přirozené obnovy v horském smrkovém lese na Trojmezné. Silva Gabreta 15, 67–84.

Baier, R., Meyer, J., Göttlein, A., 2007. Regeneration niches of Norway spruce (*Picea abies* [L.] Karst.) saplings in small canopy gaps in mixed mountain forests of the Bavarian Limestone Alps. Eur. J. For. Res. 126, 11–22.

Bergeron, Y., Harvey, B., 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. 92, 235–242.

Brang, P., 2001. Resistance and elasticity: promising concepts for the management of protection forests in the European Alps. For. Ecol. Manage. 145, 107–119.

Brokaw, N.V.L., Fraver, S., Grear, J.S., Thompson, J., Zimmerman, J.K., Waide, R.B., Everham III, E.M., Hubbell, S.P., Foster, R.B., 2004. Disturbance and canopy structure in two tropical forests. In: Losos, E.C., Leigh Jr., E.G. (Eds.), Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network. University of Chicago Press, pp. 177–194.

Bütler, R., Angelstam, P., Ekelund, P., Schlaeffer, R., 2004. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biol. Conserv. 119, 305–318.

Canham, C.D., Papaik, M.J., Latty, E.F., 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. Can. J. For. Res. 31, 1–10.

Castagneri, D., Lingea, E., Vacchiano, G., Nola, P., Motta, R., 2010. Diachronic analysis of individual-tree mortality in a Norway spruce stand in the eastern Italian Alps. Ann. For. Sci. 67, 304.

Cook, E.R., Krusic, P.J., 2005. Program ARSTAN: A Tree-ring Standardization Program Based on Detrending and Autoregressive Time Series Modeling with Interactive Graphics. Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY.

Diggle, P.J., 1983. Statistical Analysis of Spatial Point Patterns. Academic Press, London.

Dobrovolný, P., Brázdil, R., 2003. Documentary evidence on strong winds related to convective storms in the Czech Republic since AD 1500. Atmos. Res. 67–68, 95–116.

Duncan, R.P., 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dycrydioides*). N. Z. Nat. Sci. 16, 31–37.

Duncan, R.P., 1991. Competition and the coexistence of species in a mixed Podocarp stand. J. Ecol. 79, 1073–1084.

Engelmark, O., Kullman, L., Bergeron, Y., 1994. Fire and age structure of Scots pine and Norway spruce in northern Sweden during the past 700 years. New Phytol. 126, 163–168.

Fraver, S., Jonsson, B.G., Jönsson, M., Esseen, P.-A., 2008. Demographics and disturbance history of a boreal old-growth *Picea abies* forest. J. Veg. Sci. 19, 789–798.

Fraver, S., Ringvall, A., Jonsson, B.G., 2007. Refining volume estimates of down woody debris. Can. J. For. Res. 37, 627–633.

Fraver, S., White, A.S., 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. J. Veg. Sci. 16, 597–610.

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

Fritts, H.C., 1978. Tree Rings and Climate. Academic Press, New York.

Getzin, S., Dean, C., He, F.L., Trofymow, J.A., Wiegand, K., Wiegand, T., 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. Ecography 29, 671–682.

Getzin, S., Wiegand, K., 2007. Asymmetric tree growth at the stand level: random crown patterns and the response to slope. For. Ecol. Manage. 242, 165–174.

Hais, M., Jonášová, M., Langhammer, J., Kučera, T., 2009. Comparison of two types of forest disturbance using multitemporal Landsat TM/ETM plus imagery and field vegetation data. Remote Sens. Environ. 113, 835–845.

He, F.L., Duncan, R.P., 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. J. Ecol. 88, 676–688.

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

Hofgaard, A., 1993. Structure and regeneration patterns in a virgin *Picea-Abies* forest in northern Sweden. J. Veg. Sci. 4, 601–608.

Holeksa, J., Saniga, M., Szwagrzyk, J., Dziedzic, T., Ferenc, S., Wodka, M., 2007. Altitudinal variability of stand structure and regeneration in the subalpine spruce forests of the Pol'ana biosphere reserve, Central Slovakia. Eur. J. For. Res. 126, 303–313.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurements. Tree-Ring Bull. 44, 69–75.

Hunziker, U., Brang, P., 2005. Microsite patterns of conifer seedling establishment and growth in a mixed stand in the southern Alps. For. Ecol. Manage. 210, 67–79.

Janda, P., Bače, R., Svoboda, M., Starý, M., 2010. Věková a prostorová struktura horského smrkového lesa v I. zóně "Trojmezná" v NP Šumava. Silva Gabreta.

Jelínek, J., 2005. Od jihočeských pralesů v hospodářským lesům Šumavy. Ministerstvo zemědělství ČR, Úsek lesního hospodářství, Ústav pro hospodářskou úpravu lesů Brandýs nad Labem, Prague.

Jonášová, M., Matějková, I., 2007. Natural regeneration and vegetation changes in wet spruce forests after natural and artificial disturbances. Can. J. For. Res. 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. Ecol. Eng. 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. Biol. Conserv. 141, 1525–1535.

Jonsson, B.G., 2000. Availability of coarse woody debris in a boreal old-growth *Picea abies* forest. J. Veg. Sci. 11, 51–56.

Jönsson, M.T., Fraver, S., Jonsson, B.G., 2009. Forest history and the development of old-growth characteristics in fragmented boreal forests. J. Veg. Sci. 20, 91–106.

Kenkel, N.C., 1988. Pattern of self-thinning in jack-pine—testing the random mortality hypothesis. Ecology 69, 1017–1024.

Korpel, Š., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart, Jena, New York.

Kozlowski, T.T., Kramer, P.J., Pallardy, S.G., 1991. The Physiological Ecology of Woody Plants. Academic Press, Inc., San Diego.

Kräuchi, N., Brang, P., Schonenberger, W., 2000. Forests of mountainous regions: gaps in knowledge and research needs. For. Ecol. Manage. 132, 73–82.

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

Kupferschmid, A.D., Brang, P., Schonenberger, W., Bugmann, H., 2006. Predicting tree regeneration in *Picea abies* snag stands. Eur. J. For. Res. 125, 163–179.

Kuuluvainen, T., 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland—a review. Ann. Zool. Fenn. 31, 35–51.

Kuuluvainen, T., 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fenn. 36, 97–125.

Kuuluvainen, T., Aapala, K., Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J., Tukia, H., 2002. Principles of ecological restoration of boreal forested ecosystems: Finland as an example. Silva Fenn. 36, 409–422.

Kuuluvainen, T., Syrjanen, K., Kalliola, R., 1998. Structure of a pristine *Picea abies* forest in northeastern Europe. J. Veg. Sci. 9, 563–574.

Lachat, T., Bütler, R., 2009. Identifying conservation and restoration priorities for saproxylic and old-growth forest species: a case study in Switzerland. Environ. Manage. 44, 105–118.

Leibundgut, H., 1987. Europaische Urwälder der Bergstufe. Haupt, Bern.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433–445.

Loosmore, N.B., Ford, E.D., 2006. Statistical inference using the G or K point pattern spatial statistics. Ecology 87, 1925–1931.

Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can. J. For. Res. 19, 651–663.

Martikainen, P., Siitonen, J., Kaila, L., Punttila, P., Rauh, J., 1999. Bark beetles (Coleoptera, Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. For. Ecol. Manage. 116, 233–245.

Maser, C., Anderson, R.G., Cromack, K.J., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. In: Thomas, J.W. (Ed.), Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553. U.S.D.A., Portland.

Motta, R., Berretti, R., Lingua, E., Piussi, P., 2006. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. For. Ecol. Manage. 235, 155–163.

Motta, R., Edouard, J., 2005. Stand structure and dynamics in a mixed and multilayered forest in the Upper Susa Valley, Piedmont, Italy. Can. J. For. Res. 35, 21–36.

Motta, R., Nola, P., Piussi, P., 1999. Structure and stand development in three subalpine Norway spruce (*Picea abies* (L.) Karst,) stands in Paneveggio (Trento, Italy). Global Ecol. Biogeogr. 8, 455–471.

Motta, R., Nola, P., Piussi, P., 2002. Long-term investigations in a strict forest reserve in the eastern Italian Alps: spatio-temporal origin and development in two multi-layered subalpine stands. J. Ecol. 90, 495–507.

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. Biodivers. Conserv. 17, 2979–3001.

Nagel, T.A., Svoboda, M., 2008. Gap disturbance regime in an old-growth *Fagus-Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. Can. J. For. Res. 38, 2728–2737.

Nagel, T.A., Svoboda, M., Diaci, J., 2006. Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus-Abies* forest in southeastern Slovenia. For. Ecol. Manage. 226, 268–278.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics 1996. John Wiley & Sons, Inc., New York.

Penttila, R., Siitonen, J., Kuusinen, M., 2004. Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. Biol. Conserv. 117, 271–283.

Pouska, V., Svoboda, M., Lepšová, A., 2010. The diversity of wood-decaying fungi in relation to changing site conditions in an old-growth mountain spruce forest, Central Europe. Eur. J. For. Res. 129, 219–231.

Rammig, A., Fahse, L., Bebi, P., Bugmann, H., 2007. Wind disturbance in mountain forests: simulating the impact of management strategies, seed supply, and ungulate browsing on forest succession. For. Ecol. Manage. 242, 142–154.

Ripley, B.D., 1981. Spatial Statistics. John Wiley and Sons, New York.

Šamonil, P., Antolík, L., Svoboda, M., Adam, D., 2009. Dynamics of windthrow events in a natural fir-beech forest in the Carpathian mountains. For. Ecol. Manage. 257, 1148–1156.

Seymour, R.S., Hunter Jr., M.L., 1999. Principles of ecological forestry. In: Hunter Jr., M.L. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge.

Shackleton, C., 2002. Nearest-neighbor analysis and the prevalence of woody plant competition in South African savannas. Plant Ecol. 158, 65–76.

Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. For. Ecol. Manage. 128, 211–225.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.

Spiecker, H., 2003. Silvicultural management in maintaining biodiversity and resistance of forests in Europe-temperate zone. J. Environ. Manage. 67, 55–65.

Storaunet, K.O., Rolstad, J., Groven, R., 2000. Reconstructing 100–150 years of logging history in coastal spruce forest (*Picea abies*) with special conservation values in central Norway. Scand. J. For. Res. 15, 591–604.

Svoboda, M., Matějka, K., Kopáček, J., 2006a. Biomass and element pools of understory vegetation in the catchments of Certovo Lake and Plesne Lake in the Bohemian Forest. Biologia 61, S509–S521.

Svoboda, M., Matějka, K., Kopáček, J., Žaloudík, J., 2006b. Estimation of tree biomass of Norway spruce forest in the Plesne Lake catchment, the Bohemian Forest. Biologia 61, S523–S532.

Svoboda, M., 2007. Les ve druhé zóně v oblasti Trojmezné není hospodářskou smrčinou: změní se management dříve než vznikne rozsáhlá asanovaná plocha? Silva Gabreta 13, 171–187.

Svoboda, M., Zenáhlíková, J., 2009. Historický vývoj a současný stav lesa v NP Šumava kolem “Kalamitní svážnice” v oblasti Trojmezné. Příroda 28, 71–120.

Svoboda, M., Wild, J., 2007. Historical reconstruction of the disturbance regime in a mountain spruce forest landscape. In: Lingua, E., Marzano, R., (Eds.), Natural Hazards and Natural Disturbances in Mountain Forests—Challenges and Opportunities for Silviculture, IUFRO: Trento, Italy. p. 50.

Svoboda, M., Pouska, V., 2008. Structure of a Central-European mountain spruce old-growth forest with respect to historical development. For. Ecol. Manage. 255, 2177–2188.

Šantrůčková, H., Šantrůček, J., Šetlík, J., Svoboda, M., Kopáček, J., 2007. Carbon isotopes in tree rings of Norway spruce exposed to atmospheric pollution. Environ. Sci. Technol. 41, 5778–5782.

Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991. The response of sub-alpine forests to spruce beetle outbreak in Colorado. Ecology 72, 213–231.

Wallenius, T.H., Pitkanen, A., Kuuluvainen, T., Pennanen, J., Karttunen, H., 2005. Fire history and forest age distribution of an unmanaged *Picea abies* dominated landscape. Can. J. For. Res. 35, 1540–1552.

Wermelinger, B., 2004. Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. For. Ecol. Manage. 202, 67–82.

Wiegand, T., Moloney, K.A., 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104, 209–229.

Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. 21, 414–416.

Zielonka, T., 2006. When does dead wood turn into a substrate for spruce regeneration? J. Veg. Sci. 17, 739–746.

Zielonka, T., Holeksa, J., Fleischer, P., Kapusta, P., 2010. A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. J. Veg. Sci. 21, 31–42.