

Structure and origin of mountain Norway spruce in the Bohemian Forest

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ABSTRACT: Information on the historical background of the present forest conditions is needed for proper decisions on forest management. Disturbances play a major role in the formation of forest structure and composition. This paper compares the present break-up of mountain spruce stands in the Bohemian Forest (in the Šumava Protected Landscape Area) with conditions during their initiation using dendrochronological techniques. On three selected localities we established two study plots within relatively old stands of unknown origin. Stands were recently broken up by a windstorm. The present situation was described by diameter and decay class distribution. To describe the situation at the stand initiation, we cored at least 40 stems on each plot to get the age structure and growth series of trees. Disturbances were marked by discovering synchronous releases on tree-ring series. Main population waves were initiated in association with severe disturbances during a relatively short period, leading to the establishment of relatively even-aged, homogeneously looking stands. The disturbances were synchronized between plots and accounted for by historically known windstorms or bark beetle outbreaks; notwithstanding, logging as a disturbance factor is also particularly possible.

Keywords: dendroecology; natural disturbance; *Picea abies* (L.) Karst.; regeneration; stand dynamics; disturbance history

Understanding the forest dynamics (and its structural effects) is greatly needed for proper management of protected areas as well as for effective utilization of commercial areas (KIMMINS 2004). The definition of a natural range of variability is still missing for mountain Norway spruce forests in Central Europe (KULAKOWSKI, BEBI 2004). This is a problem because the degree of naturalism (based on structural attributes) is used for managing the existing protected areas and establishing or excluding others (MÍCHAL, PETŘÍČEK 1999). The disagreement about protected mountain spruce stands in the Bohemian Forest (Šumava National Park and Protected Landscape Area) is partly based on the problems raised by the relative homogeneity of these stands and their present relatively large

break up (FISCHER et al. 2002; JONÁŠOVÁ, PRACH 2004; VACEK, PODRÁZSKÝ 2008; PRACH et al. 2009), which is not consistent with the original idea of what constitutes a virgin forest.

The initial description of forest dynamics in Central Europe arises from the work of KORPEL (1989, 1995). His model of a small developmental cycle was developed mainly by studying stand structures on study plots and was used for all forest types in a similar manner. But even this author accepts the possibility of “catastrophic break up” in mountain spruce forests. Not until the last decade was it discovered – based on studies of historical documents (SVOBODA 2006), extensive structural work (HOLEKSA et al. 2007) and dendroecology (MOTTA et al. 1999; ZIELONKA, MALCHER 2009; ZIELONKA

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et al. 2010; SVOBODA et al. submitted 2011) – that this type of disturbance could naturally cause a large break up on the landscape level. Other than repeated measurements on study plots (which lasts for many decades), only reconstruction by a dendrochronological tree-ring analysis could describe the past stand development (VINŠ 1961; HENRY, SWAN 1974; OLIVER, STEPHENS 1977). Wave-regenerated stands initiated after severe disturbances in the past have subsequently a relatively homogeneous structure versus continually regenerated stands affected by disturbances of low severity (FRELICH 2002).

Disturbances play a fundamental role in vegetation dynamics. They have become the basic part of the vegetation dynamics in the last 50 years (PICKETT, WHITE 1985). The disturbance is defined as any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment. The mentioned change (resource openness) is usually followed by a release of smaller trees from suppression (growth increase) or establishment of new cohorts (LORIMER, FRELICH 1989). A few main disturbance factors exist in studies of tree population dynamics – fire, wind, insects, other pathogens and animals, including man-made harvesting (FRELICH 2002). But the attributes of a concrete disturbance regime remain unanswered – the rotation period, severity and extent of different types of disturbances occurring in a landscape (FRELICH 2002).

A part of the regeneration ecology of species could be described by the age distribution of a population (ÅGREN, ZACKRISSON 1990; HOFGAARD 1993; ENGELMARK et al. 1994; BRUMELIS et al. 2005). The knowledge of its relationship to disturbances is vital, but it is very difficult to determine the real age of a tree (DESROCHERS, GAGNON 1997; NIKLASSON 2002). Taking increment cores in higher parts of stems (stump or breast height) leads to an underestimation of tree age and dispersion of age distribution in degree of decades (DESROCHERS, GAGNON 1997; PARENT et al. 2000; GUTSELL, JOHNSON 2002; NIKLASSON 2002; PETERS et al. 2002). But instead, the aim could be to describe the origin of a stand (relationship of forest regeneration and disturbances). For this purpose, it is not necessary to obtain the real ages of trees, but it needs to get as close as possible (in time) to the disturbance. It is possible to sample trees at breast height in forest types where higher advanced regeneration is released after removing the overstorey (FRAVER, WHITE 2005a; SPLECHTNA et

al. 2005). In the case of mountain Norway spruce in the Bohemian Forest, mainly small regeneration is released after disturbance (JONÁŠOVÁ 2001; JONÁŠOVÁ, PRACH 2004; ULBRICHOVÁ et al. 2006; SVOBODA 2007; ZENÁHLÍKOVÁ, SVOBODA 2011), so we feel it is important to core trees as low as possible at stump height consistently with other authors (VEBLEN et al. 1994; MOTTA et al. 1999; D'AMATO, ORWIG 2008).

In the Bohemian Forest almost all old mountain Norway spruce stands were broken up since the end of the 1980's due to windstorms and attacks of bark beetle. A notable proportion was broken up by the Kyrill windstorm in January 2007. The goal of the work was therefore 1) to describe the structure of those disturbed stands immediately before the windstorm, and 2) to describe its origin and to compare it to the present situation. Are these stands wave regenerated or not, even-aged or multi-aged? Are present disturbances historically unique, or is the present situation comparable to the past? In particular, we will solve what may be the cause of the found disturbances, whether wind, bark beetle or human activities. We will discuss the hypothesis about the artificial origin of these forests (ZATLOUKAL 1998; VACEK, PODRÁZSKÝ 2008).

MATERIAL AND METHODS

This work was conducted within selected mountain Norway spruce stands of the Protected Landscape Area (CHKO) Šumava located in the southwestern Czech Republic in central Europe (Fig. 1). Pure Norway spruce woods occur mainly in isolated upper parts of this section of the mountain range. The tree layer is strongly dominated by Norway spruce (*Picea abies* [L.] Karst.) with only an admixture of other species (*Sorbus aucuparia* [L.], *Acer pseudoplatanus* [L.], *Abies alba* [Mill.], *Fagus sylvatica* [L.] and others) (NEUHÄUSLOVÁ, MORAVEC 1998).

Threeseperated localities of the Šumava Protected Landscape Area were selected for this study: (1) Jezerní Mt. (1,343 m a.s.l., plots JEZ1 and JEZ2) on the top of the Královský hvozď ridge, and (2) Můstek Mt. (1,235 m a.s.l., plots MUS1 and MUS2) on the top of the Pancíř ridge in the north-western range of the Bohemian Forest, and (3) Boubín Mt. (1,362 m a.s.l., plots BOU1 and BOU2) on the top of the Boubín highlands in the central part of the Bohemian Forest (Table 1). Geologically, the Bohemian Forest is a crystalline complex – the

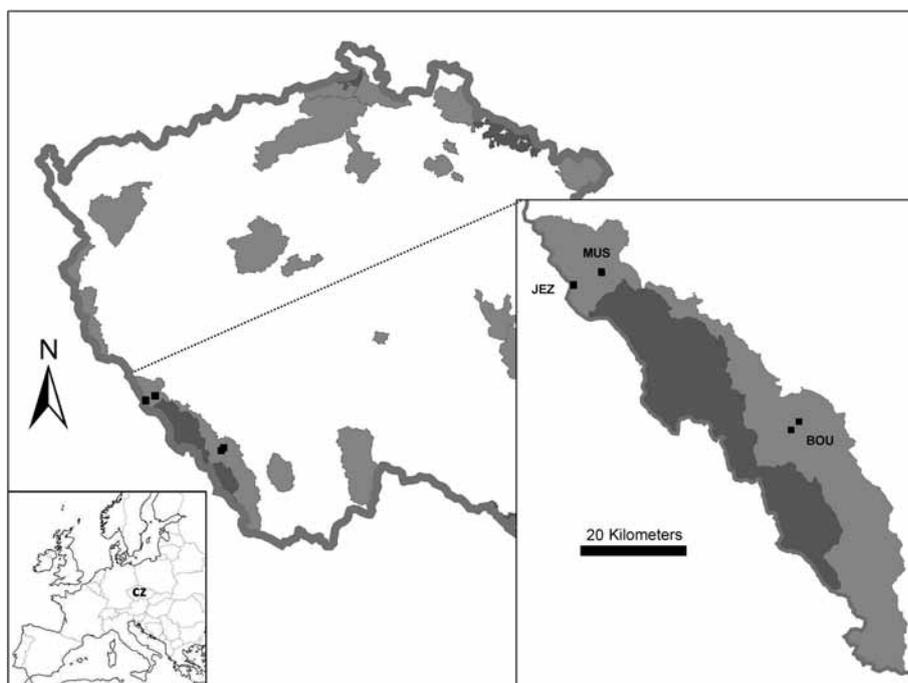


Fig. 1. Location of the study area in the Czech Republic. The Šumava Protected Landscape Area is in light grey (CENIA[®] ČSÚ, ARCDATA, AOPK ČR, MŽP; geoportal.cenia.cz). Positions of the study plots (Jezerní Mt. – JEZ, Můstek Mt. – MUS, and Boubín Mt. – BOU – see Methods) are shown by black squares

oldest (Hercynian) part of the Bohemian Massif is called Moldanubicum. This complex consists mainly of Eastern schist. Jezerní Mt. and Můstek Mt. are pure (mica schist) and Boubín Mt. is richer (gneiss) (CHÁB et al. 2007). The same situation

is found within the soil cover – from stony soil on Jezerní Mt. to podsol on Boubín Mt. (KOZÁK 2010). The climate is cold with mean annual temperature of about 4°C. The continentality increases from west to east. Mean annual precipitation

Table 1. Basic characteristics of the plots

		Locality (plot)					
		Jezerní Mt.		Můstek Mt.		Boubín Mt.	
		JEZ1	JEZ2	MUS1	MUS2	BOU1	BOU2
Altitude (m)		1,337	1,321	1,200	1,175	1,280	1,317
Longitude (m)	SJTSK	-846,106	-846,082	-840,861	-840,750	-804,794	-803,310
Latitude (m)	SJTSK	-1,131,124	-1,131,368	-1,128,668	-1,128,916	-1,158,897	-1,157,324
Spruce (percentage by number/basal area)		99.61/98.99	100	100	99.43/98.83	100	100
Additional species		rowan		fir, beech			
	density of trees (ha ⁻¹)	516	316	608	348	348	284
Living trees	mean diameter (cm)	35	40	32	40	46	51
	basal area (m ² ·ha ⁻¹)	50.65	41.45	54.82	48.18	55.58	60.31
	density of trees (ha ⁻¹)	512	448	80	244	100	144
Dead trees	mean diameter (cm)	26	31	24	22	37	33
	basal area (m ² ·ha ⁻¹)	30.36	36.64	3.93	10.17	12.63	13.25
	density of trees (ha ⁻¹)	1,028	764	688	592	448	428
Sum	mean diameter (cm)	30	35	31	32	43	45
	basal area (m ² ·ha ⁻¹)	81.01	78.09	58.75	58.35	68.21	73.57

Positions of the study plots (Jezerní Mt. – JEZ, Můstek Mt. – MUS, and Boubín Mt. – BOU – see Methods)

reaches about 1,400 mm-year⁻¹ on Jezerní Mt., over 1,200 mm-year⁻¹ on Můstek Mt. and 800–1,000 mm-year⁻¹ on Boubín Mt. (TOLASZ 2007). Vegetation communities are described as *Calamagrostio villosae-Piceetum* (with transition to *Calamagrostio villosae-Fagetum* on Můstek Mt.; NEUHÄUSLOVÁ, MORAVEC 1998).

A few authors postulated the unnatural planted origin of mountain spruce stands of the Bohemian Forest (ZATLOUKAL 1998; VACEK, PODRÁZSKÝ 2008). But in fact no direct evidence exists before the 1860s when the first management plans for large land owners of forests were made (JELÍNEK 2005). Hardly any stands older than 80 years, which were described as virgin forests on these maps, have survived to the present. And there exists a high uncertainty about the way of the origin and historical management of stands younger than 80 years on these maps.

For our study we selected forest stands of unknown origin on the three localities. Two study plots were analyzed on each locality. For Jezerní Mt. a 41–60 years old patch was found surrounded by more than 80-years-old stands on the first map from 1876 (State Archive SOA Plzeň, VS Železná Ruda, map 2). Boubín Mt. is a part of the protection forest where no logging has been set in prescription since 1858 (VANĚK 1985). The first plot on Boubín Mt., BOU1, was placed into a stand younger than 20 years on the first map from 1868. This stand was next to an area affected by the bark-beetle outbreak in the 1870's, which was subsequently logged (JELÍNEK 2005). It was not possible to find the boundary in the field. The second plot on Boubín Mt., BOU2, was placed into a stand described as being older than 80 years in 1868 (JELÍNEK 2005). Můstek Mt. was owned by the village of Javorná and no direct evidence of management exists from the 19th century (JELÍNEK 2005).

Data collection

Two 50 × 50 m study plots were established at each locality (i.e. 6 plots in total). Plots were selected in an area that was fully replaced after the Kyrill windstorm from January 2007. Salvage logging was done at all localities after the windstorm. There was an effort to meet the requirement for homogeneity and representativeness of each plot.

Electronic and laser measuring devices linked to a GIS (Field-Map[®], Monitoring and Mapping Solutions, Ltd.; www.fieldmap.cz) were used to measure the stand structures. All live and dead

trees (diameter at stump height over 10 cm) were positioned. For each tree we recorded its species, diameter at stump height (about 30 cm) and decay class based on the classification of GROVEN et al. (2002). GROVEN et al. (2002) used an eight-class scale based on the presence of bark, solidity of sapwood and heartwood and visibility of wood structures. We added to the scale the class 0 for living trees. Unlike GROVEN et al. (2002) we were not able to find any trees that could be listed in class eight (totally decayed, found by pigmented soil) due to the dense vegetation cover and soil disruption by disturbances (windstorm as well as subsequent logging). This problem is also likely responsible for the slight underestimation of further classes. Trees that died due to the windstorm in January 2007 or later were included in class 2.

The aim was to describe the state of the stands before break-up. Thus, trees in class 2, together with classes 0 and 1, were further specified as “living trees” and trees in higher decay classes were further specified as “dead trees”.

We extracted one core at stump height from each possible bole on the plots on Jezerní Mt. After salvage logging we could almost always view the pith of a stump, we focused on taking cores from the side with representative growth (in cases with excentric growth) and not affected by root swellings. We then evaluated the age structure from Jezerní Mt. and found that the average differences between all ages of the sample and subsamples diminished more slowly after taking 30–40 samples. Thus, we realized (taking the plot as a point in space) that it was sufficient to core about 30–40 trees. This number is consistent with other studies (FRELICH, LORIMER 1991; VEBLEN et al. 1994; D'AMATO, ORWIG 2008; FRAVER et al. 2009). We established a transect through the centre of each plot (i.e. 50 m long) and wide enough to include about 40 boles from which it was possible to take a core. We then extracted a core from each bole inside the transect on Můstek Mt. and Boubín Mt. in the same way as described for Jezerní Mt.

Increment cores were air-dried, attached to a wooden mount and cut with a razor-blade. The contrast was improved by moistening and impressing the chalk. Ring widths on all cores were measured to the nearest 0.01 mm using the LINTAB measuring device connected to a computer with TsapWin programme (RINNTECH, Inc., Heidelberg, Germany). Ring borders were localized using an Olympus stereomicroscope with a cross.

To append the width of each measured ring to an absolute year, it is necessary to do cross-dating

(DOUGLASS 1929). This can solve the problem of partially missing rings (missing on the core, for example PETERS et al. 2002) and move series from dead trees or trees with decayed sapwood. Cross-dating was done in Past4 programme using visual cross-dating as well as statistical tests – Gleichlaufigkeit and *t*-test of transformed series (KNIBBE 2007). Sample chronologies were plotted against the mean chronology made of series of well growing trees with wide rings (YAMAGUCHI 1991), against the mean chronology from Trojmezna Mt. in the southern part of the Bohemian Forest (JANĎA et al. 2010) and verified by the light ring of 1912 (GINDL 1999) and marked rings found by ČEJKOVÁ and KOLÁŘ (2009). Final verification was done in COFECHA (HOLMES 1983; GRISSINO-MAYER 2001). A few series which did not fit well were excluded. Missing rings were inserted and given the lowest measurable value of 0.01 mm.

To evaluate tree age, we estimated the number of rings missed in cases when the core did not pass through the pith. We estimated the distance between the first measured ring and expected pith by placing a transparent sheet with concentric circles. The number of missed rings was then acquired by dividing this distance by the mean ring width of the five rings closest to the centre.

Data analysis

There was a total of 281 series for Jezerní Mt. (plot JEZ1 – 168, plot JEZ2 – 113), 89 series for Mústek Mt. (plot MUS1 – 43 series, plot MUS2 – 46 series) and 90 series for Boubín Mt. (plot BOU1 – 46, plot BOU2 – 44). A total of 23 series of the Jezerní Mt. had rotten centres and therefore it was not possible to calculate their age. Of the remaining 258 series, 19% passed through the pith, 90% were within 14.30 mm of the pith and the maximum distance to the pith was 39.90 mm. For Mústek Mt. and Boubín Mt., 10 series had rotten centres. For the other 171 series, 51% passed through the pith, 90% were within 6.73 mm and the maximum distance to the pith was 30.45 mm.

Ring width series were used for the dating of past disturbance events. These methods are based on the knowledge that a tree accelerates its growth after its competitors are removed by a disturbance. This is called a release and is defined as a rapid, sudden and sustained growth increase. Synchronized release events indicate a relevant disturbance (LORIMER, FRELICH 1989). To filter out other changes in growth, releases are usually computed

from 10-year running means and only changes over a subjectively assessed threshold are marked (LORIMER, FRELICH 1989). We used the “absolute increase” method to determine releases (FRAVER, WHITE 2005b). Absolute growth changes were calculated for each year of each series except the first and the last 10 years by subtracting the prior 10-year mean from the subsequent 10-year mean. A year was marked as a release if the value was the maximum of a 20-year interval (± 10 year) and exceeded the threshold of +0.55 mm (JÖNSSON et al. 2009). This threshold was specified directly to Norway spruce based on experience with its growth variation (JÖNSSON et al. 2009). This threshold is equivalent to 24% of the boundary lines used for Norway spruce averaged across all prior growth classes (SPLECHTNA et al. 2005; ZIELONKA et al. 2010). Finally we checked all series and their releases visually. Releases were excluded if the growth acceleration was not obvious (the average percentage among plots was 18.4% of cases excluded) – for example growth restoration after short-term growth reduction, short-term pulses etc. Releases were also added in obvious cases (the average percentage among plots was 11.8% of cases added). Visual checking is vital in this type of work, because growth fluctuations due to environmental variation (climate, injuries, mast year etc.) have a high effect close to the specified threshold. Basically it is always a trade-off between positive and negative errors. Non-release growth changes are not related only to climate variations, which is usually used to test the criteria (NOWACKI, ABRAMS 1997; BLACK, ABRAMS 2003). There exists a great overlap with changes caused by injuries, reaction wood etc. (FRAVER, WHITE 2005b; FRAVER personal communication). To overcome the problem of subjectivity, we also defined more strict criteria to detect higher magnitude and longer duration releases (15-year means, absolute increase threshold +0.75 mm) where little subjectivity was used (on average 2.3% of cases excluded). Results (Fig. 4) showed that the dating of major disturbances was little affected by a specified threshold. Releases connected to major disturbances were both of higher magnitude and longer duration.

All releases were then counted every year and plotted proportionally to the sample depth in each year. We wanted to show the real distribution of releases and date the disturbances as closely as possible by peaks in distribution. We wanted also to determine the rate of past break-up (immediate or slower origin of stands). It is important to note that mathematically derived criteria and tree reaction

delay (mainly 1–5 years) could cause a few-year dispersion of releases in time (NOWACKI, ABRAMS 1997; RENTCH et al. 2002; JONES, THOMAS 2004). Nevertheless, we found that releases were clustered on the time axis. We then calculated also the percentage of all older trees released in specified periods and showed it above the chronology. The chronology was truncated when the sample depth dropped below 10 and the time axes were restricted to the period of main tree establishment on the plots, i.e. 1750–1929.

Nonparametric methods were used to test our results. Spearman's correlation coefficient was used to test relationships between basic characteristics from Table 1 and the Kruskal-Wallis test (subsequently also post-hoc multiple comparison tests) was employed to compare the distributions of diameters, decay classes and ages. We used the 0.05 significance level to reject the null hypothesis.

RESULTS

Structure of the tree layer

Forest stands on all plots consisted of nearly 100% Norway spruce. Basic characteristics are shown in Table 1. A relatively high variation of values was found in the case of tree densities (316 to 608 trees per hectare). If we incorporate data from the mountain spruce locality Trojmezna in the Bohemian Forest (SVOBODA 2007; JANDA et al. 2010; SVOBODA et al. 2010) and also the historical situation (i.e. dead trees), then the range is from 200 to 1,600 trees per hectare. Basal area showed less variation (note that our data were taken at stump height) – i.e. from 40 to 60 m²·ha⁻¹. This dispersion is attributable to recent mortality before the windstorm on plots JEZ2 and MUS2 and less on plot JEZ1 (Fig. 3). In these cases, it is probable that the population of trees did not fill in the space re-

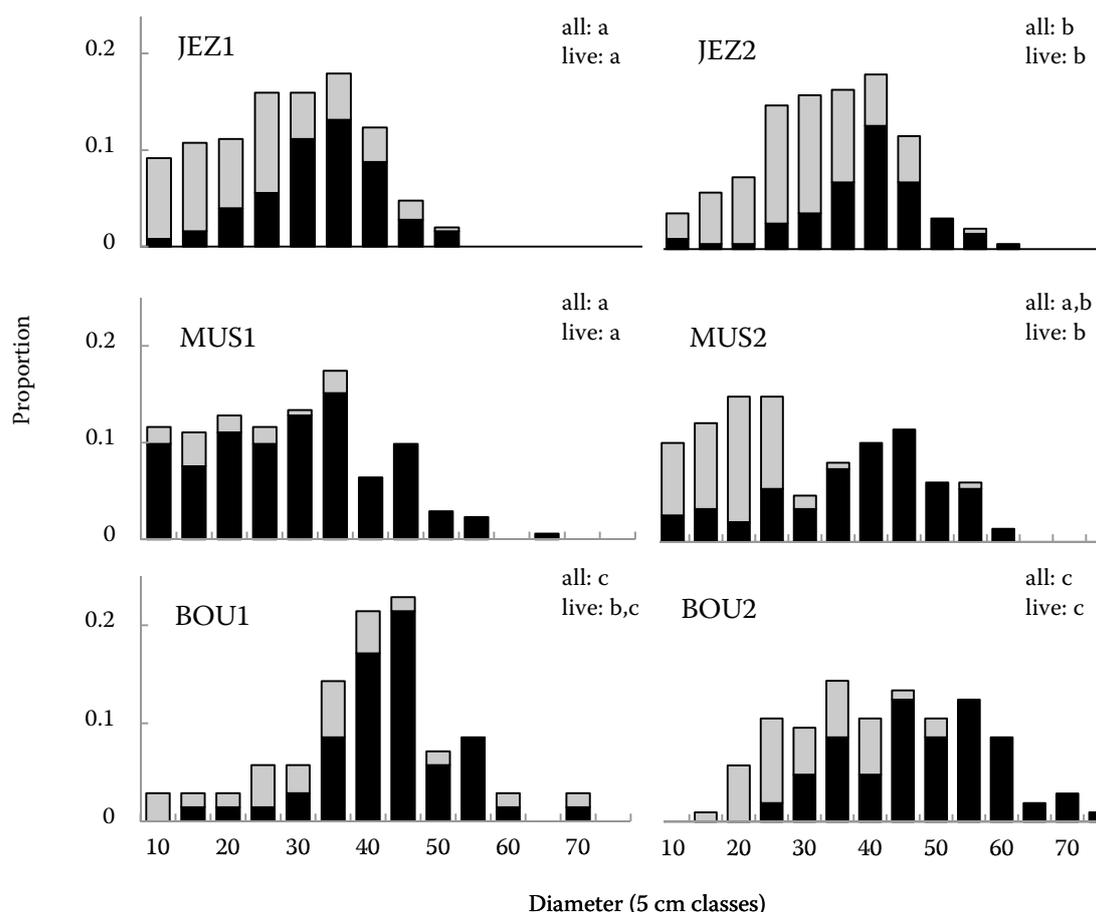


Fig. 2. Diameter distribution of living (black columns) and dead trees (grey columns) before the stand replacing windstorm from January 2007. Results of the Kruskal-Wallis test, comparing distributions of all trees and live trees between plots, are shown on the right sides of the graphs (all: $H_{5, N=936} = 127.23, P < 0.001$; live: $H_{5, N=56} = 141.23, P < 0.001$). Distributions with different letters differed significantly ($P < 0.05$)

leased by this mortality before the windstorm. After exclusion of these plots, the range of basal areas narrowed to 55–60 m²·ha⁻¹. The proportion of dead trees was higher if we used the tree number, but it was lower if we used basal areas for the computation. This means that dead trees had smaller diameters than living trees. The largest differences were on Můstek Mt. and Boubín Mt., while differences were less notable on Jezerní Mt. (Figs 2 and 3). This indicates recent mortality of thick dominant trees caused by recent disturbances before the windstorm at the latter locality and only recent self-thinning at the other localities.

Spearman's correlation coefficients were calculated for the variables in Table 1 ($n = 6$, $P < 0.05$). Trees had larger diameters on Boubín Mt. (mean diameter vs. longitude, $r = 0.83$), while more trees grew on Jezerní Mt. and Můstek Mt. A significant negative relationship was found between the tree number and their mean diameter (living as well as all trees, $r = -0.90$ and $r = -0.83$, respectively). This

is probably related to the differences in environmental conditions (Material and Methods). There was a higher proportion of dead trees on Jezerní Mt. (basal area of dead trees vs. altitude, $r = 0.89$). A positive relationship was found between the basal area of all trees and that of dead trees ($r = 0.89$). There was a negative, non-significant relationship between the basal area of living trees and the number of dead trees ($r = -0.60$).

The diameters of living trees generally showed a modal type of distribution (Fig. 2). This distribution shows a tendency to the left asymmetry on all plots. The distributions of all trees among plots differed significantly (Kruskal-Wallis test, $H_{5, N=936} = 127.23$, $P < 0.001$). A distinct diameter structure was found on Boubín Mt. with hardly any proportion of stems below 10 cm. The result evolve if we use only living trees (Kruskal-Wallis test: $H_{5, N=56} = 141.23$, $P < 0.001$). The exclusion of thin stems and development of a classical modal type continued also at the other localities. The modes developed in

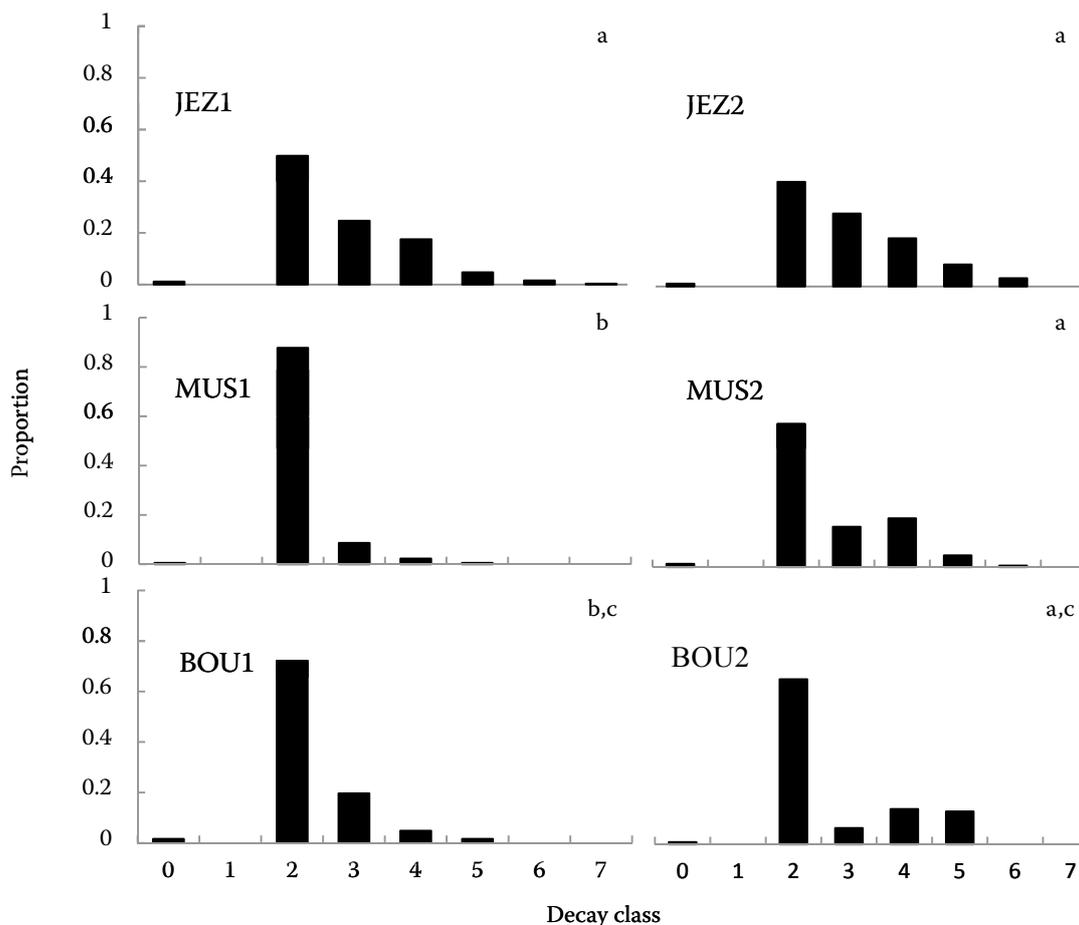


Fig. 3. Distribution of decay classes, after GROVEN et al. (2002), which show recent stand dynamics and lasting of break-up. Trees died after the windstorm in January 2007 are in class 2. The break-up was more rapid when the dominance of class 2 was stronger. Results of Kruskal-Wallis tests comparing distributions between plots are shown on the right sides of the graphs ($H_{5, N=923} = 95.56$, $P < 0.001$). Distributions with different letters differed significantly ($P < 0.05$)

the 45–50 cm class on Boubín Mt. and Můstek Mt. and in smaller classes on Jezerní Mt.

The decay class distribution shows recent stand dynamics (Fig. 3). Forests with continuous dynamics usually show a dominance of decay class 3 (GROVEN *et al.* 2002), however this was not attained on the study plots. Instead, we found a high dominance of class 2 on all plots (i.e. mainly trees destroyed by the Kyrill windstorm or after it), which indicates the unstable dynamics of these stands. The strength of this instability is described by the magnitude of the dominance of decay class 2. The distributions among plots differed significantly (Kruskal-Wallis test: $H_{5, N=923} = 95.56, P < 0.001$). There was a low amount of dead wood on Můstek Mt. and Boubín Mt. before the windstorm. Recent higher mortality (before the windstorm) was found on Jezerní Mt. This area was broken up more slowly.

Age structure and disturbances

Age distributions on the plots are closer to the modal type of distribution than to the exponential type of distribution (Fig. 4). This shows an unstable type of forest dynamics. Peaks in age distributions are quite narrow and located in only a few decades. On the other hand, the age range is from 85 to 215 years. Other smaller peaks in tree establishment could be found on four plots. The main peaks of tree establishment occurred in the 1820s on plots JEZ2 and BOU2, in the 1850s on plot BOU1, in the 1860s on plots JEZ1 and MUS1, and in the 1870s on plots MUS2 (and smaller ones also on plot BOU1). Smaller peaks occurred also in the 1780's on plots JEZ1 and BOU2, and the 1910's on plot MUS1.

Release events are clustered on the time axis (Fig. 4). Continuous polygons of release events are separated by periods with no releases. The peaks in tree establishment are closely connected with peaks in releases (i.e. with disturbances), occurring mainly in the same decade. In a few cases on Můstek Mt., the peak in ages preceded the disturbance by one decade. In one case, the peak in tree establishment was delayed one decade after the disturbance (plot BOU1, 1840–1850). Also, regeneration stopped 2 or 3 decades after the disturbance, with the exception of two plots (MUS1 and BOU1), where the origin was connected with more and separate disturbances.

The majority of trees which established before major disturbances showed suppressed growth and accessed the canopy through release. Only a few trees were left from the overstorey of the previous stand

and showed no release in the time of the main tree establishment. The proportion of trees older than the main population wave (main peak in age distribution) highly differs from 5 trees to a half of all trees. 71–94% of these older trees showed synchronized release events in the period of the peak in age distribution (Fig. 4). Sometimes it is probable that two or several close disturbance events in time caused the stand initiation. For example, there are two separated peaks on plot BOU2 in the years 1812 and 1824 or prolonged releases over more than a twenty-year period on plot JEZ1. Peaks in release chronologies were synchronized to the early 1820s (JEZ2, BOU2), early 1860s (JEZ1, BOU1), 1870s (MUS1, MUS2) and early 1920s (MUS1). Additional peaks were created in the early 1780s (JEZ1) and between the years 1836 and 1843 (BOU1).

DISCUSSION

We found structurally relatively homogeneous stands of mountain Norway spruce on the micro-scale level at the three selected localities at higher elevations of the Bohemian Forest. The tendency to the left asymmetry of diameter distributions is also a tendency towards heterogeneity. This tendency was found in more uneven-aged stands and younger stands. The distribution could also be decreasing if the regeneration could grow to the canopy in recent decades (KORPEL 1989; MOTTA *et al.* 1999; JANDA *et al.* 2010). This occurs in cases of two-layered stands (KORPEL 1989; JANDA *et al.* 2010), regenerated stands (KORPEL 1989) or early successional stands (MOTTA *et al.* 1999). This pattern was not attained on our study plots, so that no regeneration growing up to the canopy occurred since the 1920s. This is probably the cause of the visual homogeneity of these stands.

As the dynamics of dead wood follows the dynamics of living trees (SVOBODA, POUŠKA 2008), we can describe recent dynamics by the distribution of the decay classes. Two different types of pattern were found. A small portion of dead wood occurred at two localities (Můstek Mt. and Boubín Mt.) suggesting that the windstorm was the only big disturbance event which caused the present break up. On the other hand, stands were breaking up more slowly on Jezerní Mt., which lasted for about two decades (Fig. 3). This was even more evident in the work of JANDA *et al.* (2010) from Trojmezna Mt. in the southern part of the Bohemian Forest.

The detected origins of the stands show rather convergent than divergent character compared to

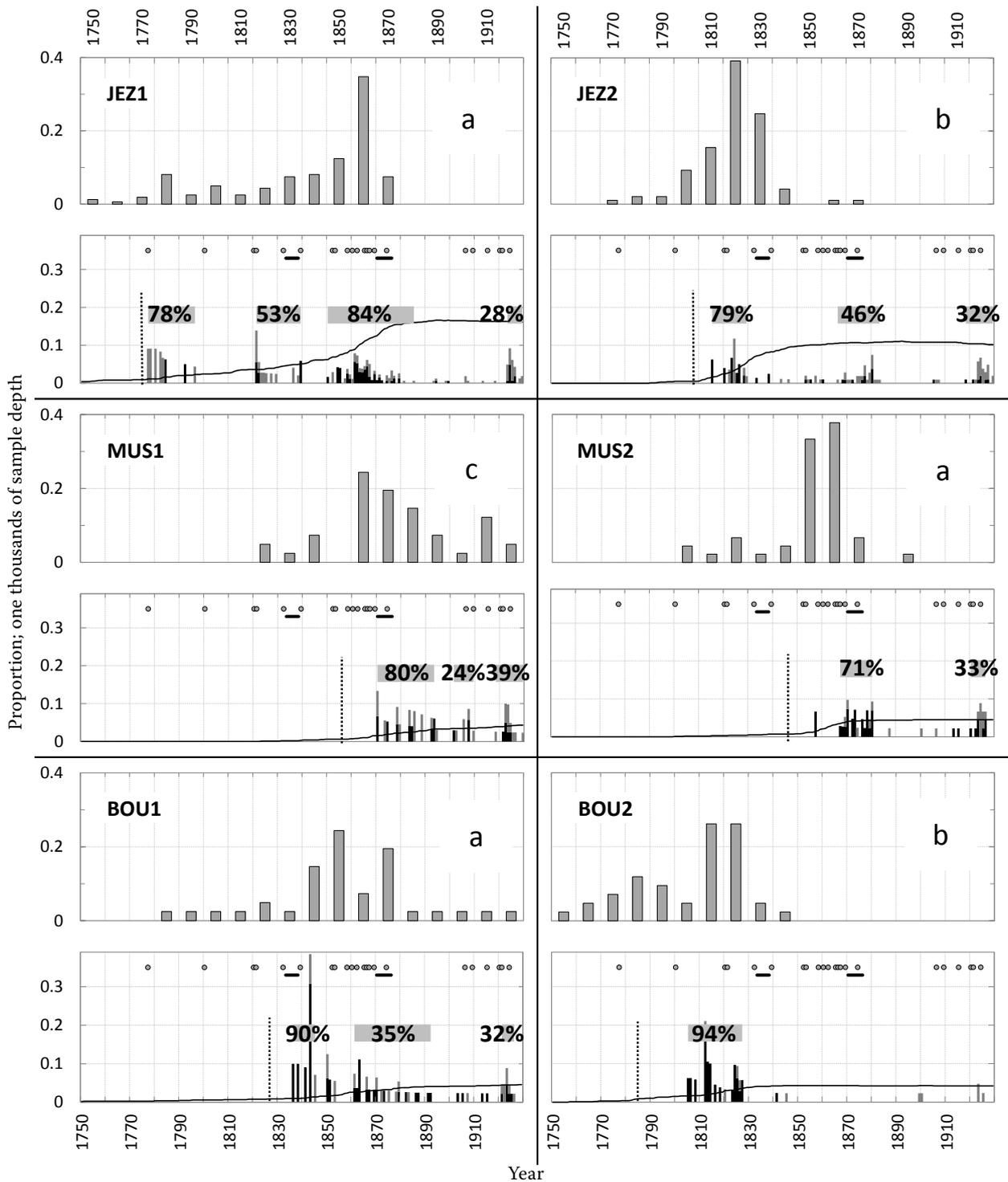


Fig. 4. Distribution of ages and release events in the period of stand establishment. Ages are summarized in 10-year classes (upper graphs, grey columns). For every year, the number of released trees is shown proportionally to the sample depth in that year (lower graphs, columns). Black columns are releases of higher magnitude and longer duration (see methods). Releases are clustered on the time axis to separated periods. The percentage of released trees in these periods is shown above. One thousandth of the sample depth is shown as lines on lower graphs. Release chronology was truncated when the sample depth dropped below 10 (indicated by a vertical dotted line). Time axes are restricted to the period of main tree establishment on the plots, i.e. 1750–1929. 5 individuals (3.11%) on plot JEZ1 and 2 individuals (4.88%) on plot BOU1 established before the year 1750. Circles on the lower graphs indicate known historical windstorms (BRÁZDIL et al. 2004) and bold lines indicate known historical bark-beetle outbreaks (SKUHRAVÝ 2002). Results of the Kruskal-Wallis tests comparing age distributions between plots are shown on the right side of the graphs ($H_{5, N=427} = 154.12, P < 0.001$). Distributions with different letters differed significantly ($P < 0.05$)

the present situation. The main population waves were relatively even-aged (two to three decades). The proportion of trees older than the main waves is dependent on the character of the preceding stand (FRELICH 2002). Only a few trees existed in the preceding understorey for more than a decade on four of the six plots. Our opinion is that this ratifies the situation known in the present structures. New, relatively even-aged stands grow up from small individuals after the breakup. These individuals have already been mainly in the understorey. Some regeneration is possible also shortly after a disturbance, but the delay is not more than a few years. A smaller proportion of individuals could be described as advanced regeneration, being higher than 0.5–1 m (JONÁŠOVÁ 2001; ULBRICHOVÁ et al. 2006; SVOBODA 2007; ZENÁHLÍKOVÁ, SVOBODA 2011). Some exceptions do exist. This could be the case for the more heterogeneous, multiple-origin stands. We found populations with clearly two peaks in the age distribution on two plots. Secondly, the present modal age distribution does not necessarily mean that no regeneration occurred after. Younger trees often experience a higher probability of mortality, thus they may not survive to the present (JOHNSON et al. 1994). This could be the explanation for the peak of dead trees in diameter distribution on plot MUS2 (Fig. 2), which could be younger trees that regenerated later. We reconstructed a disturbance from the 1920s on this plot, which caused regeneration on the first plot of this locality, MUS1.

Periods with increased numbers of release events are coincident with periods of increased recruitment and therefore the initiation of stands. These periods are separated on the time axis, which indicates that high severity disturbances regenerated these stands. Consistent with the present situation, the break-up of a preceding stand could sometimes be caused by temporally closer disturbances, and could last for two decades. But the stand initiation connected with one disturbance event was also recognized. It is important to note that small understorey saplings could increase their growth (show release) after a small canopy opening preceding the main, severe disturbance (BAČE et al. 2009).

Using only tree ring data, we could not determine which factor caused the past stand breakups. We could not distinguish between windstorm, bark beetle outbreak or harvesting. But we can use other information to make one interpretation more probable. Most disturbances were closely (scale of years) synchronized between plots and localities. And most of them are clearly accounted for by historical evidence (Fig. 4). These include

the windstorms of 1778, 1821 or 1822, 1833 and a subsequent bark beetle outbreak in 1840, several windstorms in the 1850s and 1860s, 1870 and subsequent bark beetle outbreak in 1921 or 1922 (SKUHRAVÝ 2002; BRÁZDIL et al. 2004). As an example, all three plots (JEZ1, JEZ2, BOU2), which were old enough to experience the early 1820s windstorms, indicated a disturbance during this time. Disturbances in the 1780s and 1820s initiated also the stand on Trojmezná Mt. (Svoboda et al. unpublished 2011). Less synchronized is the origin of plot BOU1 in the 1840s.

It is more difficult to analyze the possible logging of windthrows, bark beetle infested trees or survived trees, which could come after the natural event. We could perhaps get help from the information that present logging usually destroys advanced regeneration (JONÁŠOVÁ 2001; JONÁŠOVÁ, PRACH 2004). Since the second half of the 19th century, forests have been managed intensively in the Czech part of the Bohemian Forest, including the harvesting of left virgin forest (BENEŠ 1996; JELÍNEK 2005). We have evidence of the logging of trees after the bark beetle attack on Boubín Mt. (plot BOU1) in the 1870s (JELÍNEK 2005), which may also be the cause of the release peak on plot MUS1 in 1884.

Neither could we solve if all the trees regenerated naturally or were planted. Based on historical evidence the planting was carried out in the Bohemian Forest since the second half of the 19th century (JELÍNEK 2005). Therefore the regeneration of JEZ2 and BOU2 was probably fully natural. Many trees regenerated before the disturbance on the rest of plots. Underplanting is not probable on these inaccessible sites. The natural regeneration was therefore important but we do not know to what extent.

Furthermore, we were not able to solve the issue of secondary interference of the forest dynamics by humans. This interference is highly probable, but it is not clear how strongly it could affect the main pattern of the stand break up and initiation. In the past, this was mainly livestock grazing, selective logging, management of the state frontier, roads and so on (JELÍNEK 2005). Presently, human interference consists in thinning, harvesting in the neighbourhood, logging of bark-beetle infested trees, pollution and so on, some of which could increase the stand homogeneity.

CONCLUSIONS

Severe natural disturbances have played a fundamental role in forest dynamics in the upper parts of

the Šumava Protected Landscape Area. This type of stand initiation results in a relatively homogeneously looking structure, which is not a sign of planted origin. The described structure and dynamics could therefore be probably taken as a part of the range of natural variability of mountain Norway spruce forests. This knowledge is important in natural conservation and ecological forestry. The information about regeneration ecology and natural hazards of these forests could be applied also in strictly commercial forests. But more research is needed to make these issues more clear and to support our preliminary results with more replications and also to improve our knowledge of human interference.

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