Stand-replacing disturbance does not directly alter the succession of Norway spruce regeneration on dead wood

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ABSTRACT: Density of regeneration in European subalpine Norway spruce (*Picea abies*) forests is typically low with regeneration primarily located on dead or decaying wood. The post-disturbance development of this regeneration is crucial for natural forest succession. The aim was to identify the influence of disturbance on regeneration on decaying logs immediately after a severe disturbance event. Study plots were established in two subalpine spruce forests: the first, an undisturbed site located in the Hrubý Jeseník Mts. and the second site in the Šumava Mts. that has experienced recent severe disturbance. Regeneration density increased between 2008 and 2011 by 7% (0.29 individuals per square meter of log) at the undisturbed site and by 33% (3.24 individuals per square meter of log) at the disturbed site. The increased regeneration density observed at the disturbed site was mostly associated with the smallest saplings. The highest increase in regeneration density was observed on logs with the largest diameters. Three years after severe disturbance caused 100% mortality of the parent stand in the Bohemian Forest, no significant effect was recorded on the growth rate and survival of established spruce saplings on dead wood.

Keywords: decaying logs; natural regeneration; *Picea abies*

Until recently, wind disturbance and subsequent bark beetle (*Ips typographus* L.) outbreaks in central European forests were considered as a non-natural process without significant influence on natural forest succession and development (Splechtna et al 2005). Recent dendrochronological analysis (Svoboda et al. 2012; Čada et al. 2013) and studies derived from historical forest maps (e.g. Bruna et al. 2013) have shown the opposite, with forest stand structure often linked to the last severe disturbance event. These forests have been disturbed several times in the recent past by disturbance events of varying severity and this has had a major impact on stand development over the last 120 years (Bruna et al. 2013). These locations are crucial to understand forest recovery and the extent of variability in forest succession after severe disturbance events (Čada et al. 2013) which are an important driver of central European mountain spruce forest dynamics (Zielonka et al. 2010; Svoboda et al. 2012). Every disturbance event creates biological legacies that are often necessary to promote biodiversity with many species dependent on frequent disturbance events (Franklin, Frelich 2002; Čada et al. 2013). One such legacy of a disturbance event is the increased availability of decaying wood.

The density of regeneration in European subalpine spruce forests is typically low (Wohlgemuth, Kull 2002; Streit et al. 2009) with the majority of regeneration focused on favourable microsites such as dead or decaying wood. The number of spruce seedlings (*Picea abies* [L.] Karst) occupying dead wood can be up to 80% of the total stand regeneration (Svoboda et al. 2010). In these areas the issue of regeneration development and survival on decaying logs is crucial for forest dynamics. Environmental conditions change after a severe disturbance event that results in the death of parent

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stands, creating open canopy conditions that enable increased light exposure and subsequently more favourable conditions for regeneration growth (Metslaid et al. 2007). On the other hand, after a disturbance event, an increase in surface temperature (Hais, Kučera 2008) in combination with periods of drier weather in the previous years (Matějka 2011) can cause desiccation of logs and subsequent sapling mortality. Each log has different qualitative characteristics that provide different conditions for sapling growth (Zielonka 2006). Previous research shows that characteristics such as decay stage, log diameter and presence of rot fungi play an important role in seedling density (Bače et al 2012). Currently, there is a lack of research on the importance of log characteristics after a disturbance event and if these conditions change. The aim of this paper is to observe the development of natural regeneration on decaying logs immediately after 100% mortality of the parent stand. The results are compared with the development of natural regeneration of spruce on decaying logs in an undisturbed mountain spruce forest stand. The main questions are: (*i*) how has the natural regeneration developed during the three-year study period at both the disturbed and undisturbed site; (*ii*) how has the density of saplings in each height category changed; and (*iii*) has this change been influenced by type of locality, original regeneration density or other log characteristic (e.g. log diameter, ground contact, decay stage, presence and type of rot fungi or surrounding vegetation)?

MATERIAL AND METHODS

Study site. Data was collected from two subalpine spruce forests in the Czech Republic. At each site, two square plots (100 × 100 m) were established. The first site, Eustaška, is situated in the central area of the Hrubý Jeseník Mts. (north-eastern Czech Republic) in the protected area, Praděd (50°5'N, 17°15'E). The plot is situated on a gentle south-eastern slope (up to 10°) with an altitudinal range between 1,240 and 1,270 m a.s.l. The total annual precipitation at this altitude is approximately 1,200 mm and the mean annual temperature is around 4°C. Plant communities were classified as *Calamagrostio villosae-Piceetum* (Banáš et al. 2001). The stands in this area are a good representation of subalpine old-growth spruce forest, with virgin forest appearance. However, barked logs are occasionally identified as remnants of previous salvage logging in the area. According to Czech law (Decree No. 64/2011 of the Statute Book), these stands are classified as near-natural forest (Adam et al. 2011). The oldest trees in the region range in age from 260 to 300 years and are known to have survived a severe series of disturbance events between 1770 and 1840 while they were still young and adaptable trees. However, most of the trees forming the present-day canopy and upper storeys were established as a succession of a new generation of forest after this disturbance event. The current age of these trees ranges from 160 to 230 years; however, this generation has developed to create a structurally diverse and varied age stand without experiencing any large scale disturbance in the recent past (Adam et al. 2011).

The second site Trojmezná is situated in Šumava National Park in the southern Šumava Mts. The study plot is located on a gentle northern slope (up to 10°) along the mountain ridge located between Třístoličník and Trojmezná (48°47'N, 13°49'E). The altitudinal range is from 1,250 to 1,270 m a.s.l. The total annual precipitation at this altitude is approximately 1,200 mm and the mean annual temperature around 4°C. Plant communities were classified as *Athyrio alpestris-Piceetum* (Neuhäuslová 2001). There is little evidence for past anthropogenic disturbance in this region suggesting a low impact of human activity. It is therefore considered one of the largest and best conserved complexes of old-growth mountain spruce forest in the Czech Republic (Míchal, Petříček 1999). Most of the trees at this site were older than 200 years before an outbreak of bark beetle that caused 100% parent stand mortality in 2008 (Svoboda et al. 2012).

Data collection. In 2008, spruce regeneration on decaying and dead logs was recorded in both sites. All logs ≥ 2 m in length with a maximum diameter measurement of ≥ 0.15 m were analysed. Decaying logs were divided into 1.5 m long segments and the diameter of the middle of each segment measured. The position, length and diameter at both ends of the logs were measured using Field-Map (IFER-MMS, Field-Map Technology, 2009, http://www.field-map.com). For each log we recorded: decay stage ranging from 1 to 5 (Sippola, Renvall 1999); ground contact; surrounding vegetation; and dominant rot fungi (brown rot, white rot of *Phellinus nigrolimitatus* or other white rots) (Bače et al. 2012).

All saplings were recorded on each log and divided into six height categories; (1) 0–5 cm, (2) 5–10 cm, (3) 10–20 cm, (4) 20–50 cm, (5) 50– 100 cm and

(6) 100–200 cm. Current-year seedlings were not included because their count could change during the period of data collection (Mori et al. 2004). In 2011, measurements of natural regeneration were repeated at both sites.

Data analysis. Time changes in the correlation and development of spruce communities were tested using Principal Component Analysis (PCA). Species data was converted to a logarithm scale and divided into the defined height categories for two densities of saplings; density in 2008 (D_{08}) and density in 2011 (D_{11}). Density of spruce regeneration (total number of saplings) was divided by the log area (defined by the total sum of each 1.5 m segment rectangular area (middle diameter × length) and calculated for each log and height category in 2008 and 2011. To test changes in density of regeneration the same height categories as for PCA analysis were used. The response variable was defined as Density change (D_{Δ}) and calculated as a natural logarithm of the proportion of sapling density in 2011 (D_{11}) compared to the starting density in 2008 (D_{08}). D_{Δ} was tested by one-sample *t*-test assuming a normal distribution of data. The segments without regeneration in both years were omitted. D_{Δ} was tested individually for each locality (Eq. 1).

$$D_{\Delta} = \ln \frac{D_{11} + 1}{D_{08} + 1} \quad (1)$$

where:
D_{08} – density in 2008,
D_{11} – density in 2011.

The effects of explanatory variables on D_{Δ} for decaying logs were evaluated using linear models (LM). Saplings were analysed in three height classes: 0–5 cm, 5–10 cm and > 10 cm. The boundaries of height classes were determined with an emphasis on the highest resolution of the smallest individuals because of their significantly higher mortality rate (Jonášová, Prach 2004; Zenáhlíková et al. 2011). Started with a null model and then used forward selection for all variables, in particular height classes. According to these results, we assigned the significant variables to the basic model. Then backward selection was performed to create the final model. In addition a new simpler model was created in case that there was no significant difference in the former model (*F*-test).

Statistical analyses were performed using the STATISTICA version 9 software (Statsoft, Tulsa, USA) and R version 2.14.1 software (R Development core team, Wien, Austria) using libraries "MASS" and "vioplot".

RESULTS

Regeneration density on decaying logs increased during the study period at both sites. Total regeneration increased at the undisturbed site, Eustaška, by 7% (0.29 individuals per square meter of log) while regeneration at the recently disturbed site, Trojmezná, increased by 33% (3.24 individuals per square meter of log) (Table 1). Further, an increase in the number of nurse logs with at least one sapling was observed at both sites. At Eustaška nurse logs increased from 90% to 93% and at Trojmezná there was an increase from 68% to 83% (Table 2).

Table 1. Regeneration on decaying logs, density of regeneration in particular years, percentage change in density between the years 2008 and 2011 in both localities

	Eustaška		Trojmezná	
	2008	2011	2008	2011
Numbers of regeneration (indd·ha^{-1})	1,321	1,421	1,874	2,815
Total density (indd·ha^{-1})	3.75	4.04	6.45	9.69
Change in density after three years (%)		7.18		33.43

An increase in regeneration density occurred at both sites in almost all height categories with the exception of categories 0–5 cm and 5–10 cm at Eustaška, where a significant decrease in density was observed. In all other categories at this site there was a significant increase in density (*t*-test, $P < 0.05$; Fig. 1). At Trojmezná no significant increase

Table 2. The characteristics of decaying logs in both localities; number of logs without regeneration, number of logs within a particular decay stage, area and volume of logs, mean ($\bar{x}$) and median ($\tilde{x}$) values of maximum log diameter

Decaying logs	Eustaška	Trojmezná
Number	110	75
Without regeneration 2008	11	24
Without regeneration 2011	8	13
Number in decay stage 2	12	13
Number in decay stage 3	53	30
Number in decay stage 4	36	21
Number in decay stage 5	9	11
Area of logs (m^2)	351.9	290.6
Volume of logs (m^3)	87.5	120.2
Maximum log diameter ($\bar{x}$)	0.36	0.44
Maximum log diameter ($\tilde{x}$)	0.35	0.4

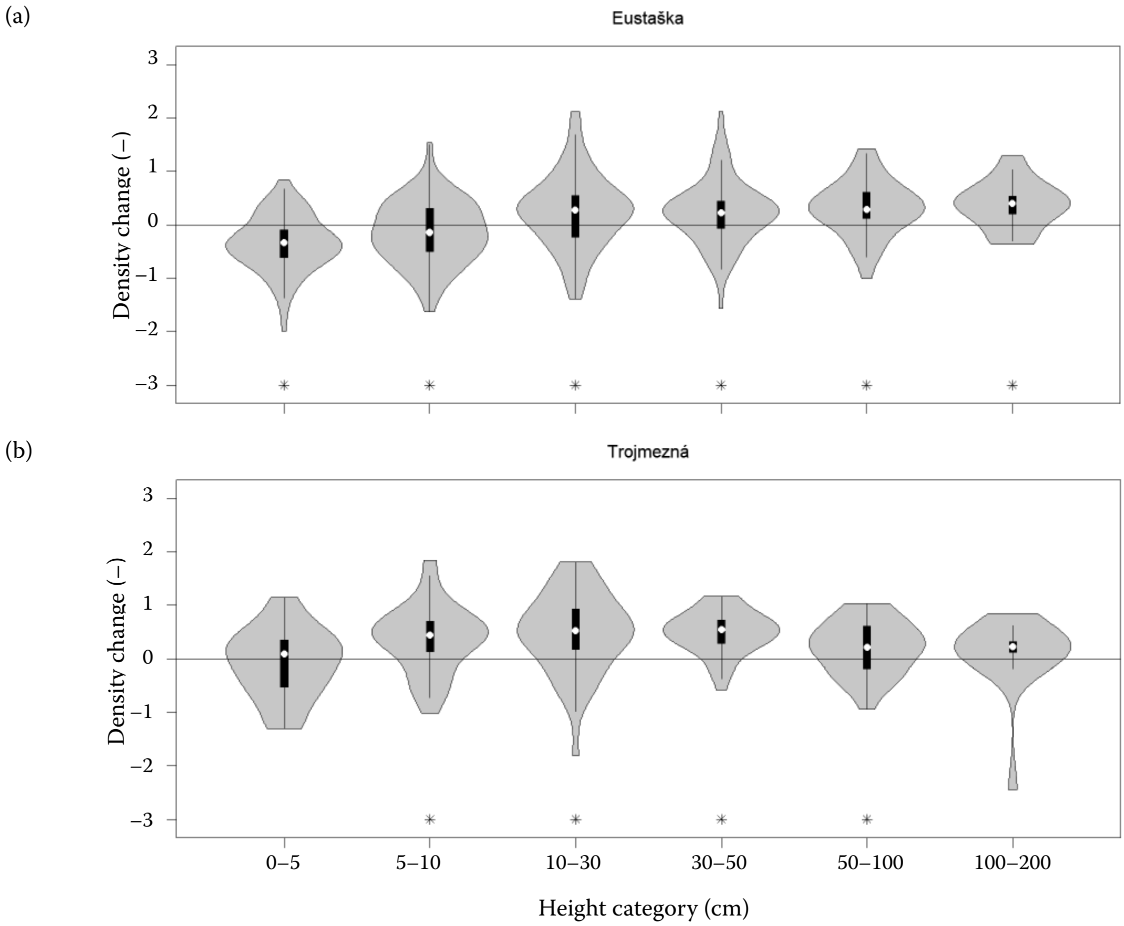

Fig. 1. Change in regeneration density in particular height categories between the years 2008 and 2011 on localities Eustaška (upper figure) and Trojmezná (lower figure). Violin plots represent median, 25% and 75% quartile, range without outliers and kernel density of change in regeneration density. Categories significantly different from zero with $P < 0.05$ are indicated by asterisks

in density was observed in the lowest and highest height categories only.

Only three of the recorded variables had a significant impact on density change (D_{Δ}): the starting density; the site Trojmezná; and the log diameter. A significant low increase in regeneration density was observed in all height categories on logs which originated with a high starting density. Higher increases in regeneration density occurred at the disturbed site, Trojmezná, in the first two height categories. In the last category, a significant impact of large diameter logs on an increase in regeneration density was observed. All values for linear models are displayed in Table 3.

The results of multivariate analysis (Fig. 2) show the successful growth of regeneration with the majority of saplings progressing to the following height category during the study period. The lowest height category of regeneration during three years is moving to the less occupied logs, against the direction of the decay stage of logs. Both locations recorded similar progression in the shift in height classification. This result shows that the effect of severe disturbance and subsequent sudden change of light conditions and thermal regime has a low effect on the growth of saplings which were previously established before the disturbance event, independently of their starting height. Further, the effect has no influence on the colonization of new, less decayed logs. An identical position in the highest height category on the disturbed site Trojmezná shows a reduction in the height increment of the highest saplings.

DISCUSSION

Although disturbance events often result in a sudden change in environmental conditions such as increased light availability (Rammig et al. 2006), our results did not show any significant difference in the development and mortality of spruce regeneration on dead or decaying logs in disturbed and undisturbed mountain spruce for-

Table 3. Results of linear models, the table shows impact of variables on change of regeneration density on decaying logs in three height categories

	Height categories					
	0–5 cm		5–10 cm		10–200 cm	
Starting density$_{08}$	−0.2058	< 0.001	−0.1556	< 0.001	0.0676	< 0.001
Locality Trojmezná	0.3670	< 0.001	0.4437	0.0001	–	n.s.
Diameter of logs	–	n.s.	–	n.s.	0.0009	0.009
Ground contact	–	n.s.	–	n.s.	–	n.s.
Decay stage	–	n.s.	–	n.s.	–	n.s.
Surrounding vegetation	–	n.s.	–	n.s.	–	n.s.
White rot	–	n.s.	–	n.s.	–	n.s.
Brown rot	–	n.s.	–	n.s.	–	n.s.
Phellinus nigrolimitatus	–	n.s.	–	n.s.	–	n.s.
R^2	0.457		0.295		0.226	
n	118		109		130	

n.s. – not significant

est. At both sites, successful growth and development indicated by saplings progressing to the following height categories were observed. In the undisturbed site, Eustaška, the amount of light exposure should be considerably lower due to the dense stand conditions of the parent stand and could affect the growth rate. However, stands in these subalpine spruce forests allow for continuous sapling growth because the canopy in these forests is not fully closed allowing sufficient light to penetrate to the logs for successful sapling development and regeneration (Kathke, Bruelheide 2010). Improvement of light conditions in disturbed sites does not have an immediate effect on the height growth of saplings and it can take several years for the post-disturbance conditions to take effect (Metslaid et al. 2005). This is probably the main reason why the variation between the two sites is small. In addition, there was no increase in mortality of saplings on the logs in disturbed area, as expected (Kathke, Bruelheide 2010). This is probably because during bark beetle

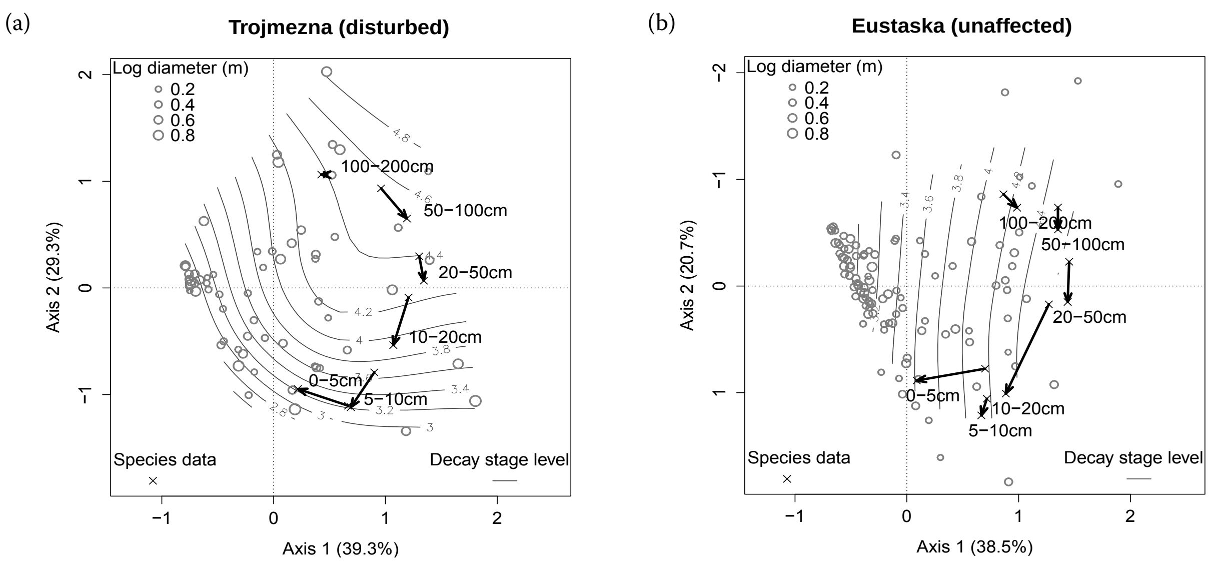

Fig. 2. Principal Component Analysis (PCA) at (a) disturbed site and (b) unaffected site. Species data (crosses) are density of spruce regeneration in the height categories in 2 years. The arrow always points from the original height class in 2008 to the new height class in 2011. Samples (decaying logs) are marked with brown circles, size of circles increases with log diameter. Isolines show the gradient of decay stage (2–5). The arrangement of height classes indicates the direction of the succession of spruce. In both localities we can see progress of succession in three years

outbreaks, snags with branches create shade, at least in the first few years after the disturbance, and provide protection against temperature extremes and potential drought (Jonášová, Prach 2004).

The total number of saplings on decaying logs increased at both sites. There was a substantial increase in the number of saplings recorded in Trojmezná, in all height categories between 2008 and 2011. The high number of saplings in the first categories (0–5 cm, 5–10 cm, 10–30 cm) is in line with the findings of Heurich (2009), who suggested that environmental conditions during a succession of bark beetle outbreak are the same as the environmental conditions for the previous year and that spruce stands are able to maximize seed production just before they die. The decrease in the number of saplings in the two lowest categories at the undisturbed Eustaška site was probably caused by relatively low seed production due to a lack of environmental stress (Hanssen 2003) and because of sapling mortality. Seed supply is irregular in these areas (Šerá et al. 2000) and seeds have a low germination capacity (Nilsson et al. 2002). Some of these saplings developed and moved to the following height categories but a considerable amount of saplings died. In areas of subalpine spruce forests extremely high mortality of spruce regeneration is often observed a few years after germination (Jonášová, Prach 2004; Zenáhlíková et al. 2011). Saplings have to survive low temperatures, thick layer of long-lasting snow cover, lack of light and moisture (Cunningham et al. 2006). With increasing growth of spruce saplings and increased height increment (Metslaid et al. 2007) they develop resistance and sapling stability (Hanssen 2003; Grassi et al. 2004; Zenáhlíková et al. 2011). Mortality or violation (e.g. breakage or dried terminal shoot) of higher saplings in disturbed stands can be caused by maturation feeding (*Ips typographus*), fall of snags, windfall or fraying by ungulates (own observation). These are potential reasons for the lack of development in regeneration density in the final height category in Trojmezná.

Impact of variables on changing density

The starting density (D_{08}) had a significant impact on the development of regeneration density and number of saplings in all three height categories. The suggested cause is the high mortality of saplings in the younger stages of development (Zenáhlíková et al. 2011). Most of the saplings had a clustering pattern because of the favourable characteristics of the decaying logs (Bače et al. 2012). The majority of the favourable logs were already occupied, so the chance for establishment and survival of new seedlings is low. The aggregation of saplings on logs can result in higher interspecific competition (Kuuluvainen, Kalmari 2003) with a growing number of saplings on decaying logs leading to a higher mortality rate (Harmon, Franklin 1989; Holeksa 2001) when seedlings have to compete for light, water, space and nutrients (Nilsson et al. 2002).

The significant impact of Trojmezná locality on regeneration density, observed in the first two categories (0–5 cm, 5–10 cm), is probably as a result of the mast year following the bark beetle outbreak. Improved light conditions could ensure a higher rate of sapling survival (Brang 1998). A further important variable for sapling establishment, growth and survival is the diameter of the decaying logs (Takahashi 1994). This is in line with our results where the largest increase in height regeneration (> 10 cm) was observed on logs with the larger diameter. Larger logs support sapling abundance (Bače et al 2012) because of the larger area available for sapling establishment (Holeksa 2001). These logs, compared with the smaller diameter logs, provide more stable temperature and humidity conditions (Harmon et al. 1986). Larger logs also protect saplings against competition from surrounding vegetation (Harmon, Franklin 1989; Jonášová 2001) and the competitive pressure of vegetation on the log surfaces is moderate, without significant impact on regeneration development (Zielonka, Piatek 2004). Takahashi (1994) found that small diameter logs (< 0.2 m) do not provide a favourable environment for regeneration of spruce (*Picea glehnii* Mast.).

CONCLUSION

Results show that the development of spruce regeneration on decaying logs three years after disturbance is similar to regeneration in an undisturbed locality. The effect of a severe disturbance event does not have an essential influence on the growth and survival rate of spruce saplings. Under both conditions, saplings grow and progress to subsequent height categories. At both locations there is an increase in the total number of saplings with a high increase in regeneration density at the disturbed site, Trojmezná, and on logs with larger diameter.

Three years after the total mortality of the parent stand caused by a bark beetle outbreak, the strong effect of disturbance on regeneration and succession has not yet occurred. It can be suggested that three years are a too short time for observing significant differences between the disturbed and undisturbed sites.

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