



Natural regeneration in Central-European subalpine spruce forests: Which logs are suitable for seedling recruitment?

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ABSTRACT

Decaying logs form the major seedbed for trees in European subalpine *Picea abies* forests. However, many aspects related to seedling colonization pattern on logs remain unclear. The aim of this study was to analyze the relationships of *P. abies* (Norway spruce) seedling (height <15 cm) and sapling (height ≥ 15 cm) densities on decaying logs in relation to stage of wood decay, log diameter, ground contact of decaying log, assumed cause of tree death, presence of species of wood-decaying fungi and coverage by surrounding plants in the subalpine old-growth forests of the Bohemian Forest and Ash Mountains, in the Czech Republic. We have focused on how logs with different origin differ in their properties and how these properties influence seedling abundance. Seedling densities peaked on the medium-decayed logs and decreased thereafter. Sapling densities continually increased as the decay progressed. Seedling and sapling densities followed negative binomial distributions, with many logs of all decay stages having low regeneration densities. The degree of ground contact, white-rot-causing *Armillaria* spp. presence, white-rot-causing *Phellinus nigrolimitatus* presence and log diameter were positively related to both seedling and sapling density. Also tree death as a result of wind uprooting was positively related to sapling density. Conversely, the presence of brown-rot-causing *Fomitopsis pinicola* and tree death as a result of bark beetle attack were negatively related to regeneration densities. The low cover of vegetation from sides positively affected seedling density; however, heavily covered logs were less occupied by seedlings. Our study provides evidence that large logs originating from wind uprooting or butt rot infection are most appropriate for retention to promote natural spruce regeneration in managed subalpine spruce forests.

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1. Introduction

Decaying logs, stumps and other woody remnants are suitable seedbeds for tree seedlings. This self-producing system of woody microsites for seedlings is found mainly for conifers and to a lesser extent, for broad-leaved species (Bellingham and Richardson, 2006; Lonsdale et al., 2008). The dependence of seedling recruitment on dead wood has been reported from various ecosystems and the largest dependence has been reported in the genus *Picea*, particularly in subalpine forests of North America, Europe and Japan (Lonsdale et al., 2008). In European subalpine forest, populations of *Picea abies* seedlings occupying dead wood microsites may account for more than 50% of total regeneration, even in semi-natural forest affected by timber extraction (Bače et al., in press; Svoboda et al., 2010). The total dependence of *Picea jezoensis* and *Picea glehnii* seedlings on dead wood was reported in conifer-

ous forests of Japan (Nakagawa et al., 2001; Narukawa and Yamamoto, 2002; Narukawa et al., 2003; Takahashi et al., 2000). Interestingly, in Swedish boreal forests, *P. abies* logs were found to be the most suitable substrate for *P. abies* seedlings as well as the seedlings of broad-leaved species, whereas the logs of broad-leaved species were almost unoccupied by seedlings (Hofgaard, 1993). On the other hand, *Picea sitchensis* seedlings occupied logs of other coniferous species in the Pacific Northwest (Harmon and Franklin, 1989).

The succession pattern of spruce seedlings on logs in relation to their decay stage was examined in the subalpine coniferous forests of Japan (Mori et al., 2004; Narukawa et al., 2003; Takahashi et al., 2000) and Poland (Zielonka, 2006). The pattern was similar in both regions. Seedling establishment on logs starts during the second decade after tree death in the subalpine spruce forests of Central Europe (Zielonka, 2006). At this time, litter and humus improve nutrient and moisture conditions for survival and growth of seedlings on logs (Harmon, 1987, 1989b; Takahashi et al., 2000). The optimum period for seedling emergence and survival occurs before mosses completely cover logs (Iijima and Shibuya, 2010; Iijima et al., 2007; Zielonka and Piatek, 2004). The colonization of logs

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by bryophytes increases seed retention; however, an excessively thick moss layer negatively affects the emergence and survival of current-year seedlings (Harmon and Franklin, 1989; Iijima and Shibuya, 2010; Takahashi et al., 2000). The number of seedlings and saplings growing on logs increases during the decomposition process. After the peak of seedling density, the seedling establishment rate slightly decreases due to intraspecific and interspecific competition with herbs and dwarf shrubs (Mori et al., 2004; Nakagawa et al., 2003; Zielonka, 2006). The end of the seedling establishment period is more variable than the start, depending largely on the variability in the time period before complete decomposition (Harmon, 1989a; Holeksa et al., 2008; Zielonka, 2006) since the seedling recruitment occurs on logs in the most advanced stages of decay and its rate is still greater than on the bare ground (Zielonka and Piatek, 2004).

Results by Harmon (1989a) indicate that spruce seedling density is very variable within all decay stages of logs and has to be essentially affected by other properties of logs. The influence of these properties has not yet been sufficiently researched. A range of organisms, of which wood-decomposing fungi play a major role, change the chemical composition and the structure of wood (Rayner and Boddy, 1988). Wood is decomposed by fungi resulting in different types of rot (Rypáček, 1957; Schwarze et al., 2000). Fungal species composition can differ considerably among spruce logs resulting in a varying prevalence of either white- or brown-rot (Pouska et al., 2011; Renvall, 1995). It is likely that the type of fungal rot determines seedling establishment, growth and survival; however, only few references to this relationship are found in literature. Vacek (1982) stated that wood affected by brown-rot fungi is more suitable for the establishment of *P. abies* seedlings than wood affected by white-rot fungi. He explained this by the absorbent, sponge-like properties of brown-rotted wood, which allows it to maintain higher moisture content during dry periods (Blanchette, 1980). However, Lička (2002) found that wood affected by white-rot fungi had greater *P. abies* seedling densities. The diameter of log is another rarely studied variable. Only Takahashi (1994), investigating seedling density, reported that small-diameter fallen logs (<20 cm) do not provide a suitable substrate for *P. glehnii* seedlings. Changes in bark cover on logs of different tree species may also lead to various patterns of natural regeneration establishment and survival since bark fragmentation kills a large proportion of seedlings on *P. sitchensis* logs (Harmon, 1989a). Iijima and Shibuya (2010) reported that recently fallen logs with bark and no moss or thin moss cover (<20 mm) appear to be the most suitable substrates for the regeneration of *P. jezoensis* in Japan.

The retention of logs in managed forests can support spruce regeneration. In Japan, Nakagawa et al. (2001) demonstrated that selection cutting in the sub-boreal forest of Hokkaido resulted in the reduction of *P. jezoensis* seedling numbers since the amount of dead wood, the crucial regeneration substrate for *P. jezoensis*, was reduced. Nakagawa et al. (2001) stressed that forest management policy needs to be changed to retain sufficient amounts of suitable dead wood. Studies evaluating the best conditions for seedling recruitment are needed to aid forest managers in decision-making, in terms of which dead wood is the most suitable for retention and therefore what type of dead wood management is sufficiently effective in supporting natural regeneration along with minimizing economic losses.

With the exception of the stages of log decay, existing knowledge about the properties of logs is largely deficient and limited to few regions (Iijima and Shibuya, 2010; Iijima et al., 2007; Mori et al., 2004; Takahashi et al., 2000). No research for treating multiple log characteristics in relation to regeneration was conducted in Central Europe. Therefore, in this study, we focused on Norway spruce seedling and sapling densities on decaying logs in relation to: log diameter, stage of wood decay, ground contact, assumed

cause of tree death, species of wood-decaying fungi and coverage by surrounding plants. We examined which characteristics influence the colonization pattern of Norway spruce seedlings on logs in two subalpine old-growth forest stands. The critical new point of our study is the study of a range of log variables, most of which has not yet been evaluated. We have focused on the origins of logs to examine how logs with different origins vary in their properties and how these properties influence seedling and sapling abundance.

2. Methods

2.1. Study sites

This study was conducted in two subalpine spruce forests in the Czech Republic. The first site, Trojmezna, is situated in the southern part of the Bohemian Forest (Šumava; 48°47'N, 13°49'E) in the south-western part of the country. Subalpine spruce forests are found between 1150 and 1450 m a.s.l. The altitude of our study plots ranges from 1220 to 1270 m. The aspect is northern on a gentle slope (up to 8°). The mean total annual precipitation is approximately 1300 mm and the mean annual temperature is approximately 3.5 °C (period 1961–2000, Climate Atlas of Czechia). Maximum snow depth is about 2 m. The bedrock is coarse-grained granite (Kopáček et al., 2002). Plant communities were classified as *Athyrio alpestris-Piceetum* (Neuhäuslová and Eltsova, 2003) with high fern *Athyrium distentifolium* undergrowth. The area of interest was established as a natural reserve in 1933 and it became a part of Šumava National Park in 1991. Norway spruce (*P. abies*) and the less abundant rowan (*Sorbus aucuparia*) dominate the forest (Svoboda and Pouska, 2008). The majority of trees on the site were more than 200 years old (Svoboda et al., 2011). According to the Natural Forests' Databank of the Czech Republic, the stands were classified as natural forests with low human influence in the past (Vrška et al., 2004). The stand adjacent to nature reserve from down slope was established in the second half of the 18th century following stand replacing disturbance (Svoboda et al., 2010). The canopy closure for the study plots was 26% in 2005 (Bače et al., 2009).

The second site of interest, Eustaška, is situated in the central part of the Ash Mts. (Hrubý Jeseník; 50°5'N, 17°15'E) in the north-eastern part of the Czech Republic. Subalpine spruce forests occur between 1050 and 1350 m a.s.l. in these areas. The altitude of our study plots ranges from 1220 to 1250 m. The aspect is south-eastern, on a gentle slope (to 10°). The total annual precipitation is approximately 1300 mm and the mean annual temperature is approximately 3 °C (period 1961–2000, Climate Atlas of Czechia). Maximum snow depth is around 2 m. The bedrock is chlorite-sericite phyllite and quartzite. Plant communities were classified as *Calamagrostio villosae-Piceetum* (Banaš et al., 2001) with *Vaccinium myrtillus* undergrowth. The old-growth forest (50 ha) where the study site is located has been officially protected since 1969. The stands are dominated by Norway spruce (*P. abies*) and are classified as near-natural forest, according to the Natural Forests' Databank of the Czech Republic (Vrška et al., 2004). The canopy closure for the study plots was 39% in 1999 (unpublished results). The densities and height structures of regeneration on logs, stumps and non-woody microsites at both sites have been described in detail in Bače et al. (in press).

2.2. Data collection

Two, closely situated, 1 ha permanent plots (100 × 100 m) were selected at both sites. The plots were selected in an undisturbed natural forest to minimize human influences such as logging or

salvage logging where logs would have been removed or debarked. The sampling was carried out at the end of the growing season in 2008. Logs of length ≥ 2 m and diameter at larger end ≥ 0.1 m originating from stumps, snags or living trees which occurred within the plot, were sampled. Position, length and the diameters at both ends of the logs were measured using Field-Map (IFER-MMS, Field-Map Technology, 2009, <http://www.field-map.com>).

To examine which properties of decaying logs affect natural regeneration, all spruce individuals were counted. Those that had established by the end of the last growing season were allocated into height classes (0–4; 5–9; 10–14; 15–19; 20–30; 30–40 cm; etc.). Current-year seedlings were not included, since their numbers could change during the data collection. Natural regeneration growing on the root plates of uprooted trees was not included. The seedlings of other rarely occurring tree species (*S. aucuparia*, *Pinus sylvestris*, and *Betula pendula*) were not included. The age of the tallest individual of natural regeneration on each log was estimated. The age estimation was based on the number of verticils and terminal bud scars visible on the aboveground and, eventually, underground stem in the cases of individuals with adventitious roots formation above the hypocotyl region (Bače et al., in press; Zielonka, 2006).

Decay stage, ground contact, surrounding vegetation, dominant rot fungi on log and assumed cause of tree death were recorded for each log. The decay stage was assessed according to Sippola and Renvall (1999), where the determination of decay is primarily based on the depth of penetration of an iron spike. The determination of ground contact was based on the length of log connected with the ground. The degree of surrounding vegetation was designated by the area of log covered by vegetation. The determination of dominant rot fungi was based on the single presence of dominant fungal species – *Armillaria* spp., *Phellinus nigrolimitatus* and *Fomitopsis pinicola*. We chose these three fungal species because of their frequent occurrence at the sites (Pouska et al., 2010) to assess the influence of fungal rot type on regeneration density and development. If any other fungal species dominated a log or if there was any combined presence of abovementioned species, they were recorded as “other species”. The presence of fungal species on the logs was determined, based on both the occurrence of sporocarps and their typical rot. The logs were also classified according to cause of tree death, such as: bark beetle (mainly *Ips typographus*, Lausch et al., 2011), competition, butt rot, windthrow and undetermined origin. The determination of cause of tree death and all other characteristics describing the properties of logs are listed and explained in Table 1.

2.3. Data analysis

The densities in each height class of regeneration were calculated as the number of individuals per square metre of log. The area of log was calculated as the area of trapezoid. The logarithmically transformed densities of individuals stratified to height classes were analysed using indirect (unconstrained) ordination method to display similarities in their distribution. Principal component analysis (PCA) was performed on samples split by site. On the basis of the PCA results, we decided to group the response variable into two height classes (<15 and ≥ 15 cm) and analyse the pooled sample of both sites with the variable representing particular site. The high densities of smaller regeneration occurred on different logs than high densities of taller regeneration at both sites. We chose the boundary of 15 cm since this value divided regeneration into two equally wide groups in the space of PCA diagram. Therefore, the number of seedlings <15 cm and number of saplings ≥ 15 cm were used as two response variables.

The effects of explanatory variables (Table 2) on seedling and sapling number were evaluated using generalized linear models

(GLMs) with a negative binomial error structure and log link function. The area of log was incorporated into the model as offset term to compensate for the variable size of samples (Faraway, 2006). The inclusion of the area as offset term results in fitting a model for the rate of occurrence. Therefore, the terms seedling and sapling density instead of number are used when interpreting GLM results. The correct interpretation of the predicted response to the level of factor is the number of individuals per log with this particular level. Model selection was performed using the Akaike information criterion (AIC) in a forward stepwise selection procedure, starting with the null model (with offset term). The AIC enables models to be compared taking into account the total explanatory power of the model and the number of variables in the model. The AIC is defined as -2 maximized log-likelihood + 2 number of parameters. The AIC therefore penalizes models with more variables. The procedure stops when the AIC cannot be improved. The model with the lowest absolute value of AIC is the most parsimonious. The quadratic terms of predictor variables were incorporated into models (as a separate choice without fixation to linear term) to detect possible non-linear effects. The significance of differences among levels of factors was tested using the method of posterior combination. The levels were merged if their merging did not cause significant change in a model using Chi-square test. We tested for differences in the effect of predictor variables between seedlings and saplings using parallelism tests. All predictors, factors and response variables are summarized in Table 2.

Spearman's rank correlation was used to analyse the relationships between predictor variables and the causes of tree death. The statistical analyses were performed using the software Canoco for Windows 4.5 (ter Braak and Šmilauer, 2003) and the software R version 2.11.1 (R Development core team, 2010) using libraries “MASS” and “vioplot”.

3. Results

The total number of Norway spruce individuals on all 398 logs was 7532 (without current-year seedlings) and the corresponding area of logs was 1499.4 m². No regeneration was found on 103 logs, 1–10 individuals were found on 152 logs and 143 logs had more than 10 seedlings or saplings. The highest number of individuals on a single log was 565. Therefore, the distributions of both the density of seedlings and saplings were over-dispersed with many low (including zero) values at all decay stages examined (Fig. 1). The over-dispersion of the sapling density was higher than the over-dispersion of the seedling density (Table 3). Mean seedling and sapling density was 3.0 and 2.0 individuals per square metre of log, respectively.

Seedlings begin to appear at a rather low abundance in decay stage 2. The highest seedling densities occurred at the decay stages 3 and 4 and decreased in decay stage 5. The sapling density continually increased with the decay progression (Fig. 1). The age of the tallest individual depended on the decay stage of a given log since the median age of the tallest individuals increased with the log decay progression (Kruskal–Wallis test; $P < 0.001$, Fig. 2).

The model for the seedling density explained less variability than the model for the sapling density (Table 3). The decay stage was not significant for the seedling density. In contrast, the effect of decay stage on sapling density was significant. Sapling density increases non-linearly with increasing decay stage, as demonstrated by the negative quadratic fit of the decay stage in the model (Table 3). The steep increase of sapling number with decay progress slows down between decay stages 4 and 5, where the model predicts the maximal values of sapling number. Both seedling and sapling density were positively related to diameter at larger end of

Table 1
Characteristics recorded on logs.

Characteristic	Description
Decay stage	The stage of decay on a five-degree scale according to Sippola and Renvall (1999) using an iron spike (length 20 cm, max. diameter 7 mm): 1 – Recently dead trunk/piece of wood; wood is hard (spike penetrates only a few mm into the wood), completely covered with bark, fresh phloem present in at least some places 2 – Wood mostly hard (spike penetrates 1–2 cm into the wood), most of the bark left (though not necessarily for bark beetle-infested trunks), fresh phloem absent 3 – Wood partly decayed on the surface or in the centre (spike penetrates 3–5 cm into the wood), large pieces of bark usually loosened or detached 4 – Most of the wood soft throughout, the whole spike (15–20 cm) penetrates into the wood (depending on wood diameter). However, the central parts can remain hard, while the surface layers of the wood can be missing 5 – Wood very soft, disintegrates when lifted; trunk usually covered by a vegetation layer
Ground contact	Ground contact (1–4): 1 – The log touches the ground with less than ¼ of its length 2 – ¼ to ½ of the log on the ground 3 – Up to ¾ of the log on the ground 4 – The log lies on the ground for more than ¾ of its length
Surrounding vegetation	Area of the log covered by vegetation (1–4): 1 – Up to 5% of the log covered from the sides 2 – 6 to 25% of the log covered 3 – 26 to 50% of the log covered 4 – More than half of the log's length covered by vegetation
Dominant rot fungi	<i>Armillaria</i> spp. – log was dominated by <i>Armillaria</i> spp. (rot and/or rhizomorphs) <i>Phellinus nigrolimitatus</i> – log was dominated by <i>Phellinus nigrolimitatus</i> <i>Fomitopsis pinicola</i> – log was dominated by <i>Fomitopsis pinicola</i> Other species – log was dominated by other species or there was any combined presence of abovementioned species
Cause of tree death	Bark beetle – recorded if a log originated from a typical clumped group of dead mature trees Competition – a log originating from a tree that had been likely to grow under the dense canopy prior to its death Butt rot – recorded if a sporocarp and/or typical rot of a root and butt parasite was found near the base of a lying tree Windthrow – uprooting of live trees Undetermined – recorded if the cause of tree death was not obvious

Table 2
Variables used in the generalized linear models. Response variables, predictor variables and levels of factors with their characteristic values.

Variable type	Variables	Values (Units)	Mean	SD ^a	MT ^b	ME ^c	Dif. ^d
Response	Seedling (<15 cm) number	0–401 (–)	11.2	30.6	15.9	6.7	0.002
	Sapling (≥15 cm) number	0–230 (–)	7.7	20.7	10.1	5.3	0.699
Predictor	Decay stage	2; 3; 4; 5	3.42	0.93	3.36	3.48	0.211
	Site (Trojmezná – Eustaška)	0 = Tr.; 1 = Eu.	0.51	0.50	0.0	1.0	–
	Diameter at larger end	0.10–1.10 m	0.40	0.19	0.44	0.37	0.005
	Ground contact	1; 2; 3; 4	3.19	1.04	3.11	3.27	0.218
	Surrounding vegetation	1; 2; 3; 4	2.28	1.09	2.81	1.76	<0.001
Factor	Dominant rot fungi:	Factor (4 levels)					
	<i>Armillaria</i> spp.	0; 1	0.14	0.34	0.16	0.11	0.154
	<i>Phellinus nigrolimitatus</i>	0; 1	0.11	0.32	0.17	0.07	0.001
	<i>Fomitopsis pinicola</i>	0; 1	0.08	0.26	0.08	0.08	0.932
Factor	Other species	0; 1	0.67	0.47	0.59	0.74	0.001
	Cause of tree death:	Factor (5 levels)					
	Bark beetle	0; 1	0.07	0.25	0.11	0.02	<0.001
	Competition	0; 1	0.13	0.34	0.10	0.16	0.096
	Butt rot	0; 1	0.11	0.31	0.11	0.10	0.791
Windthrow	0; 1	0.10	0.30	0.10	0.10	0.921	
Undetermined	0; 1	0.60	0.49	0.57	0.62	0.337	

^a Standard deviation.^b Mean for Trojmezná.^c Mean for Eustaška.^d *P*-value of difference among variable from Trojmezná and Eustaška calculated using Mann–Whitney *U* test.

log. The seedling density increased more steeply with increasing diameter than sapling density (Parallelism test; $P = 0.047$). The positive effect of ground contact on spruce density was confirmed by both seedling and sapling models with similar estimates (Parallelism test; $P = 0.380$). The significant positive linear term of surrounding vegetation on seedling density along with negative quadratic fit indicate that the effect of vegetation from sides is non-linear. The influence of surrounding vegetation has a unimodal course with peak between 6% and 25% of area covered by

side vegetation. No effect of surrounding vegetation on sapling density was demonstrated. The variable representing site was the only one predictor variable which was not significant in both models.

A significant effect of fungal rot on spruce densities on logs appeared in both seedling and sapling models. The presence of *Armillaria* spp. or *P. nigrolimitatus* rot had a positive significant effect on seedling as well as sapling density, when compared to logs dominated by *F. pinicola*. Brown-rot-causing *F. pinicola* negatively

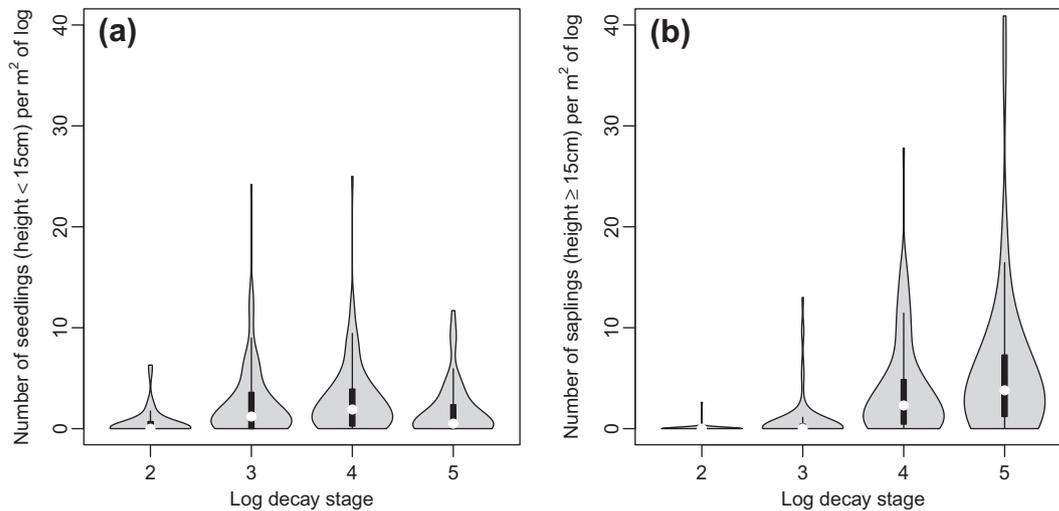


Fig. 1. The density of seedlings (a) and the density of saplings (b) vs. the decay stage of logs. The figure shows that seedling density and sapling density distribution is over-dispersed at all decay stages. Seedling density increased until decay stage 4 and slightly decreased at decay stage 5. Sapling density continually increased with decay progress. A violin plot represents median, 25% and 75% quartiles, range without outliers and Kernel density estimation of regeneration densities.

Table 3

GLM results of the effects of variables on the number of spruce seedlings (individuals <15 cm) and saplings (individuals \geq 15 cm) followed by predicted means of response for levels of two factors. The abbreviation “Sig.” indicates that factor was chosen to the model. Different lower case letters indicate significant differences ($P \leq 0.05$) among levels according to the method of posterior combination. The dispersion parameter is the aggregation value with lower values indicating a higher degree of over-dispersion (aggregation) in distribution of response variable.

	Seedlings	Saplings
<i>Parameter estimate</i>		
Site (Trojmezna – Eustaška)		
Decay stage		6.53
(Decay stage) ²		–0.68
Diameter at larger end	2.12	0.94
Ground contact	0.50	0.45
Surrounding vegetation	0.62	
(Surrounding vegetation) ²	–0.15	
Dominant rot fungi	Sig.	Sig.
Cause of tree death	Sig.	Sig.
<i>Mean no of individuals per log</i>		
<i>Armillaria</i> spp.	25.8 ^a	11.8 ^a
<i>Phellinus nigrolimitatus</i>	27.1 ^a	35.8 ^a
<i>Fomitopsis pinicola</i>	3.5 ^b	0.3 ^b
Other species	7.0 ^b	5.4 ^c
Bark beetle	1.6 ^a	0.0 ^a
Competition	4.2 ^b	3.2 ^b
Butt rot	40.7 ^b	6.8 ^b
Windthrow	14.1 ^b	14.3 ^c
Undetermined	8.7 ^b	11.4 ^b
Null deviance (df)	530.9 (397)	695.1 (397)
Residual deviance (df)	417.2 (386)	340.3 (386)
Explained variability	0.21	0.51
Dispersion par. of null model	0.49	0.21

affected regeneration density, especially in the case of sapling density, where logs decayed by this fungus significantly differed from logs with *Armillaria* spp., *P. nigrolimitatus* as well as from logs dominated by other species (Table 3). The logs hosting *P. nigrolimitatus* or *Armillaria* spp. had more than seven times higher seedling densities than logs hosting *F. pinicola*. This disproportion was even more pronounced in sapling model, where logs with *P. nigrolimitatus* had more than one hundred times higher sapling density than logs with *F. pinicola*. A significant difference between *Armillaria* spp. and *P. nigrolimitatus* was not found, although logs decayed by *P. nigrolimitatus* had approximately three times higher sapling densities than logs decayed by *Armillaria* spp.

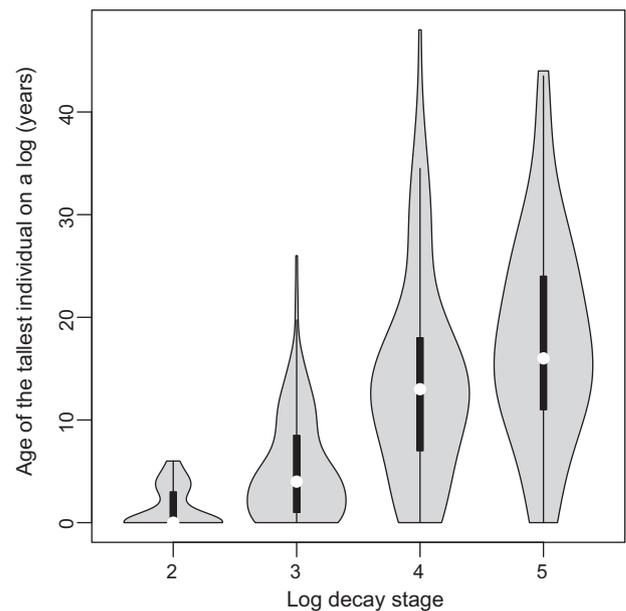


Fig. 2. The relationship between the age of the tallest individual on a particular log and the decay stage of a log showing increasing median age of the tallest individuals with decay progress. A violin plot represents median, 25% and 75% quartiles, range without outliers and Kernel density estimation of ages.

The cause of tree death also affected both seedling and sapling densities. However, only one significant difference in the seedling model was found, namely between logs originating from trees killed by bark beetles and all the other logs with other origin. This difference was confirmed in the sapling model and, in addition, there was demonstrated a positive effect of logs originating from trees that died as a result of wind uprooting. Logs originating from trees that died as a result of a butt rot and wind uprooting had higher seedling and sapling densities than logs originating from trees dying as a consequence of competition and markedly higher densities than logs originating from trees killed by the bark beetles. For other predicted means for each level, see Table 3.

Logs with various causes of tree death differed in some characteristics. Logs originating from trees that died as a result of the bark

beetle infestation were less frequently occupied by *Armillaria* spp. and were more frequently occupied by *F. pinicola*. The logs which originated from trees that died because of competition were smaller, were less frequently occupied by *Armillaria* spp. and less frequently occupied by *F. pinicola*. The logs originating from butt rot were thicker and were frequently occupied by *Armillaria* spp., and those originating from wind uprooting were thicker and frequently decayed by *F. pinicola*. For other correlations, see Table 4.

4. Discussion

4.1. Seedling colonization pattern

The colonization pattern of seedlings on logs in relation to their decay stage found in this study was similar to those found in the subalpine coniferous forests of Japan (Mori et al., 2004; Narukawa et al., 2003; Takahashi et al., 2000) and Poland (Zielonka, 2006). The median age and the number of seedlings growing on the logs increased with the progression of decomposition (Figs. 1 and 2). Regeneration densities decreased at the most advanced stages of decay due to intraspecific competition and interspecific competition with herbs and dwarf shrubs (Mori et al., 2004; Nakagawa et al., 2003; Zielonka, 2006; Zielonka and Piatek, 2004). Nevertheless, it is worth emphasising that regeneration densities are variable within all decay stages of logs (Fig. 1).

The mean regeneration density (total number/total area) on *P. abies* logs was 5.2 m^{-2} (this study; including current-year seedlings) and 5.9 m^{-2} recorded in the study from Poland (Zielonka, 2006). However, Iijima et al. (2007) reported 24.8 m^{-2} on *P. jezoensis* and *Abies sachalinensis* logs and Harmon (1989a) reported approximately 40 m^{-2} on *P. sitchensis* logs. These differences may have arisen due to both various site specific conditions and various log properties. The forest age and disturbance regime also affect regeneration density and height structure and dead wood quality and quantity. Light is a crucial factor that is related to forest dynamics and affects regeneration process. Unfavourable light conditions are the limiting factor for the growth of seedlings and saplings under closed canopies of subalpine spruce forest (Bače et al., 2009; Holeksa et al., 2007; Svoboda et al., 2010). The time period for surviving under dense canopy is limited (Kobe and Coates, 1997); therefore some older seedlings are replaced by a new cohort after a subsequent mast year (Zielonka, 2006). The period of this limitation is well documented on our one-hectare study plot on Trojmezna, where almost no saplings have exceeded the height of 2 m during the recent 100 years (Janda et al., 2010). When upper tree layer is disturbed, increased light will result in greater asymmetric competition among regeneration. The recruitment of new seedlings is also reduced by expanding forest floor vegetation

(Holeksa, 2003). The vegetation might even affect the abundance of seedlings on logs (Table 3). Consequently, the total number of seedlings starts to decrease (Jonášová and Prach, 2004).

The process leading to seedling and sapling density studied on logs consists of seed interception, retention, germination, early post-emergence mortality, later mortality rate and growth rate. It is difficult to decide, which factors are mostly responsible for regeneration densities, in which phases, and to what extent. For instance, the aspects influencing interception of seeds are not sufficiently known in subalpine forests. Spruce seeds, deposited during winter time, are often blown over the frozen snow surface. The logs arising over the snow cover likely can trap these seeds (Baier et al., 2007). Freshly fallen stems with no signs of decomposition have a small number of crevices where seeds can intercept and retain. Therefore, the decay, litter accumulation and moss colonization progress can improve seed trapping potential of young logs (Harmon, 1989b; Iijima et al., 2007). In contrast, early post-emergence mortality rate of *Picea jezoensis* var. *hondoensis* seedlings increase with progressing wood decay in subalpine forest of Central Japan (Mori and Mizumachi, 2005). In the same region, it was found that differences in initial survivorship was the main factor in the creation of seedling-substrate associations (Mori and Mizumachi, 2005; Mori et al., 2004). Therefore, in the following discussion, we attribute the reasons for different regeneration densities especially to initial survivorship.

4.2. Diameter, organic matter supply and moisture stability of logs

The diameter at a log's larger end had a positive relationship with seedling and sapling densities (Table 3). Therefore, larger logs supported seedling abundance substantially more than it would simply correspond to their area increment. Takahashi (1994) stated that small-diameter fallen logs (<20 cm) do not provide a suitable substrate for *P. glehnii* seedlings, regardless of the surrounding vegetation type. In addition, Harmon and Franklin (1989) did not find any relationship between the increase of the dead wood above ground level and seedling density in their experimental study. Therefore, although larger logs do favour seedling abundance through reducing interspecific competition, they also provide better conditions for natural regeneration since their moisture conditions are more stable than in smaller logs (Renvall, 1995). Increased log diameter results in a smaller surface to volume ratio exposing a smaller portion of wood to drying. Drought stress can be one of the causes of low seedling density (Narukawa et al., 2003; Takahashi et al., 2000). However, the effect of diameter on seedlings was significantly steeper than its effect on saplings. This can indicate that intraspecific competition amongst natural regeneration can be more intense on logs with larger diameter; both

Table 4

Spearman's rank correlation coefficients between the levels of factor cause of tree death and other predictor and factor variables on logs.

	Bark beetle	Competition	Butt rot	Windthrow	Undetermined
Site (Trojmezna – Eustaška)	-0.19***	0.03	-0.01	-0.01	0.05
Decay stage	-0.27***	-0.02	-0.22***	-0.10	0.35***
Diameter at larger end	0.09	-0.33***	0.31***	0.17***	-0.12*
Ground contact	-0.25***	0.03	-0.20***	-0.13**	0.31***
Surrounding vegetation	0.00	0.05	-0.05	0.00	-0.02
<i>Armillaria</i> spp.	-0.14**	-0.15**	0.32***	0.04	-0.05
<i>Phellinus nigrolimitatus</i>	-0.10	-0.05	-0.05	-0.07	0.15**
<i>Fomitopsis pinicola</i>	0.41***	-0.15**	0.03	0.18***	-0.23***
Other species	-0.07	0.11*	-0.10*	0.07	-0.02

Bold values are significant at *P*-values of 0.05 or lower.

No asterisk: *P* > 0.05.

* 0.01 < *P* ≤ 0.05.

** 0.001 < *P* ≤ 0.01.

*** *P* ≤ 0.001.

because of higher densities and because of less growth-space per individual outside the area of log. Optimally distributed individuals on the area of narrow rectangle have more free space outside this rectangle than individuals of the same density on the area of a wider rectangle.

The significant influence of surrounding vegetation with unimodal course indicates that when logs are situated in places without any cover of vegetation from the sides, they are less occupied by seedlings than logs under conditions of moderate vegetation shading. In contrast, high cover of side vegetation has a negative effect on seedling density. Based on the significant unimodal fit of surrounding vegetation and positive effect of log-to-ground contact on seedling densities (these two variables were positively correlated, result not shown), it seemed that seedlings which regenerated on younger (more elevated and moderately decayed logs) were favoured by greater shading of side vegetation and also by the supply of litter from surrounding plants. The survival and growth of seedlings are enhanced on logs supplemented with organic matter. The litter improves nutrient and moisture conditions (Harmon, 1987, 1989b; Takahashi et al., 2000), which in turn, can reduce drought stress. As the log becomes more decayed, it gets nearer to the ground, the depth of the litter layer therefore, increases (Harmon, 1987; Harmon and Franklin, 1989) and the effect of surrounding vegetation changes from positive to negative.

4.3. Fungi and rots

We discovered a positive effect of the presence of *Armillaria* spp. and *P. nigrolimitatus* on seedling and sapling densities compared with *F. pinicola*. Brown-rot-causing *F. pinicola*, in particular, negatively affected sapling density, when logs prevalently decayed by this fungus significantly differed from logs with *Armillaria* spp. and *P. nigrolimitatus*. Logs with *P. nigrolimitatus* had more than one hundred times higher sapling density than logs with *F. pinicola*. It is important to note that the sporocarps and the decay patterns of *P. nigrolimitatus* start to appear on the surface of logs from the decay stage 3, while *Armillaria* spp. and *F. pinicola* start from decay stage 2 (Pouska et al., 2011; Stokland and Kauserud, 2004; Ylisirniö et al., 2009). Nevertheless, logs decayed by *P. nigrolimitatus* had approximately double the sapling densities of all logs in decay stage 5; although the logs of decay stage 5 had the highest sapling density of all decay stages (Fig. 1). It appears that the presence of *P. nigrolimitatus* is crucial in facilitating high seedling densities on decaying logs.

We are unable to decide which features of rots are more species-specific and which properties can be simply attributed to brown- and white-rot type. For instance, no cation concentration trends were found to be unique for group of brown- or white-rot fungi (Ostrowsky et al., 1997). However, there are properties that are typical for each group and have possible effects on seedling colonization patterns. The lower suitability of wood subjected to brown-rot fungi, with regard to seedling establishment and survival, can be caused by a lower mechanical stability of such logs (Goodell, 2003), lower nitrogen fixation rates (Jurgensen et al., 1989), lower pH (Rypáček, 1957) and a lower water-soluble nutrient content (Takahashi et al., 2000). The wood decayed by *Armillaria* spp. can supply a higher concentration of Ca, Mg and K cations to seedlings as opposed to *F. pinicola* (Ostrowsky et al., 1997). The reason for the suitability of logs with *P. nigrolimitatus* for regeneration survival might be the mechanical stability of its white-pocket rot, which is characterized by spindle-shaped zones of white fibres surrounded by sound wood (Blanchette, 1980). This solid structure can reduce toppling of trees, a phenomenon reported by Harmon (1989a). We also believe that mycorrhizal assemblages are important for seedling establishment and survival. Differences in mechanical and chemical properties of logs,

in addition to various interactions between wood-decomposing and mycorrhizal fungi (e.g. Dighton et al., 1987; Lindahl et al., 1999; Wallander et al., 2006) are likely to affect the formation of mycorrhizae. However, conditions influencing the colonization of logs by mycorrhizal fungi have not been sufficiently studied (but see e.g. Goodman and Trofymow, 1998; Iwański and Rudawska, 2007; Lepšová, 2001; Rajala et al., 2011; Tedersoo et al., 2003).

The significant effect of the cause of tree death indicates that there is reduced regeneration density on logs originating from bark-beetle induced mortality. The logs affected by the bark beetle attack are commonly decayed by less suitable *F. pinicola* rot (Table 4; see also Jankovský et al., 2002; Pouska et al., 2011; Schroeder, 2007) since the bark beetles facilitate the entry of *F. pinicola* spores into infested trees (Persson et al., 2009, 2011; Pettey and Shaw, 1986). In addition, bark beetle infestation creates larger canopy openings, and the logs situated in an open space are exposed to higher temperature and moisture fluctuations. These conditions under the large canopy openings can be the additional reason for lower regeneration density on logs originating from bark-beetle induced mortality.

If the presence of *P. nigrolimitatus* in logs is a major cause of enhanced Norway spruce seedling densities, logging is likely to have negative effects on the natural regeneration since *P. nigrolimitatus* is very sensitive to logging disturbance in managed forests, where even seemingly suitable logs are almost unoccupied by this species (Stokland and Kauserud, 2004). Wood-decaying fungi play an important role in the self-producing system of woody microsites for Norway spruce seedlings. This complex system can easily be disturbed by wood removal. The restoration potential of this compound self-producing system of microsites in human-altered forests can be limited by the ability of sensitive fungal species to re-colonize these forests (e.g. Edman et al., 2004a,b).

5. Conclusions

This study provides evidence that spruce seedling densities are very variable within all decay stages of logs and are additionally affected by log diameter, ground contact of decaying log, species of wood-decaying fungi and coverage by surrounding plants. Logs originating from butt-rot were larger and were more frequently occupied by *Armillaria* spp. Logs originating from wind uprooting were also larger. These properties are considered to be favourable for abundant seedling recruitment. In contrast, there was reduced occupation by seedlings on logs originating from trees killed by bark beetles since most of them were being decayed by brown-rot-causing *F. pinicola*, which is less suitable for spruce regeneration. Logs originating from trees which died because of competition were less suitable for seedlings because of their smaller size. It is recommended that the logs created as a result of butt rot and windthrow should be retained to support successful natural regeneration in managed forests naturally dominated by Norway spruce.

We recommend using smaller segments of logs as sampling units (instead of whole logs; as in Iijima et al., 2007) in future research since sampling whole logs did not appear to record the variability in major properties along the log. In addition, closer focus should be made on the early and medium decay stages, during which the majority of spruce seedlings appear to establish.

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