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Density and Height Structure of Seedlings in Subalpine Spruce Forests of Central Europe: Logs vs. Stumps as a Favourable Substrate

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Decaying logs and stumps provide an important seedling substrate in natural subalpine forests. However, only stumps present such a role in managed forests. The aim of this study was to assess the differences in the process of seedling colonization between logs and stumps. The study was carried out in the Czech Republic, in two old-growth subalpine spruce forests located in the Bohemian Forest and Ash Mts., dominated by *Athyrium distentifolium* Opiz and *Vaccinium myrtillus* L. undergrowth, respectively. Norway spruce (*Picea abies* (L.) Karst.) regeneration growing on logs, stumps and non-coarse woody debris (CWD) microsites was surveyed. Regeneration (height 0–2.0 m) densities exceeded 5000 individuals per ha on both sites. The average density of *P. abies* regeneration per square meter of substrate was 0.3-5.7-19.6 and 0.5-3.8-11.0 on non-CWD microsites, logs and stumps, located in *A. distentifolium* and *V. myrtillus* undergrowth, respectively. Stumps and non-CWD microsites dominated by *V. myrtillus*, supported a higher proportion of taller seedlings per plot compared to the small seedlings growing on logs and non-CWD dominated by *A. distentifolium* ground-cover. The disproportion in regeneration densities between the stumps and the original logs decreased with increasing stages of decay. The tallest regeneration growing on stumps (root-soil plates) was significantly older than that growing on the logs (stems). Based on these two latter findings, the stumps appeared to provide suitable seedling substrates several years earlier than the logs did. Therefore, we conclude that the stumps play a more important role (relative to their covered area, 21–28 $m^2 ha^{-1}$) in terms of suitable microsites for regeneration, than the logs do.

Keywords coarse woody debris, microsite, natural regeneration, Norway spruce, *Picea abies*
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1 Introduction

Coarse woody debris (CWD) is an integral component of forest ecosystems and is important for various forest processes and functions such as forest health (Zhou et al. 2007) and maintaining biodiversity (Pouska et al. 2010). CWD also creates seedbeds for seedling establishment. One of the first studies on the role of CWD for regeneration was performed by Arnborg in Swedish subalpine forests during the 1930s (Jonsson and Hofgaard 2011). Thereafter, the suitability of CWD for tree establishment has been documented in different ecosystems around the world (Lonsdale et al. 2008). Studies have shown that tree species with smaller seeds establish on CWD more often than those with bigger seeds (Lusk 1995, Christie and Armesto 2003, Mori et al. 2004). The favourable 'seedbed effect' created by CWD is more common for conifer species, especially though for the genus *Picea* and *Tsuga* (Harmon et al. 1986, Lonsdale et al. 2008). The proportion of individuals growing on CWD is most significant in subalpine spruce forests and this significance increases with increasing altitude (Kupferschmid and Bugmann 2005, Vorčák et al. 2006, Holeksa et al. 2007), increasing density of undergrowth vegetation type (Sugita and Tani 2001, Narukawa and Yamamoto 2002, Sugita and Nagaike 2005), increasing level of snow accumulation (Sugita and Tani 2001, Sugita and Nagaike 2005) as well as with the increasing absence of exposed rocks (Sugita and Tani 2001). The total dependence of spruce seedlings on CWD was recorded in coniferous forest in Japan with dwarf bamboo undergrowth (Takahashi et al. 2000, Nakagawa et al. 2001, Narukawa and Yamamoto 2002, Narukawa et al. 2003). The ability of woody species to establish on CWD increases their competitive advantage within the boreal forests (Hofgaard 1993), mixed mountain forests (Szewczyk and Szwagrzyk 1996, Baier et al. 2007) and wetland forests where the soil substrate of the forest floor is saturated (Sharitz 1996).

The influence of the first growing season following seed germination is crucial for the development of regeneration on CWD. The germination percentage is not dependent on the microsite type; however mortality is considerably higher among the regeneration growing directly on the forest floor during the first growing season (Narukawa and Yamamoto 2002, Mori et al. 2004, Mori and Mizumachi 2005). This is mainly due to lower moisture availability (Greene et al. 1999, Mori et al. 2004, Iijima et al. 2006). Autumn mortality caused by litter accumulation (DeLong et al. 1997, Simard et al. 2003) and winter mortality caused by snow gliding (Baier et al. 2007) also play important roles. Furthermore, competition amongst the natural regeneration of tree species, herbs and/or mosses on the forest floor is another reason why seedling establishment is better on CWD microsites (Harmon and Franklin 1989, Narukawa and Yamamoto 2002, Sugita and Nagaike 2005). Seedling establishment on logs starts early, especially when the time needed for the whole log to decompose is considered (Takahashi et al. 2000, Mori et al. 2004, Zielonka 2006, Iijima and Shibuya 2010). Seedling establishment often commences prior to the complete moss colonization of free niches on the log (Zielonka and Piatek 2004, Iijima and Shibuya 2010). The number of seedlings growing on the logs increases as the decomposition progresses; however, the number of smaller seedlings slightly decreases at the most advanced stages of decay due to intraspecific and interspecific competition with herbs and dwarf shrubs (Nakagawa et al. 2003, Mori et al. 2004, Zielonka 2006). Nevertheless, the competitive rate is still lower on logs in the most advanced stages of decay than on the ground (Zielonka and Piatek 2004). This is perhaps due to the continuous creation of patches of bare, decomposed wood suitable for new seedling establishment via physical and chemical forces during the decay process (Zhou et al. 2007). Seedling survival on CWD can also be positively affected by: connection with mycorrhizal fungi (Lepšová 2001), more favourable nutrient supply (Zimmerman et al. 1995, Brunner and Kimmins 2003, Baier et al. 2006), protection against soil-borne pathogens (Lonsdale et al. 2008) and protection against browsing when branches accumulate (Lonsdale et al. 2008).

Numerous studies have focused on the role of nurse logs, or nurse logs and stumps together, as favourable substrates for natural regeneration; however, studies comparing the role of logs and stumps as seedling substrate are rather rare. Nakagawa et al. (2001) reported four times larger spruce seedling densities on stumps compared to logs in semi-natural sub-boreal forest of Hokkaido. Hofgaard (1993) stated that there were more mature trees in central Sweden growing on stumps when compared to logs; however, seedlings strongly prevailed on logs. Kathke and Bruelheide (2010) found, in near-nature Norway spruce forest in Germany, that a higher number of taller seedlings grew on stumps compared to logs, as opposed to smaller seedlings.

The importance of stumps which have been cut, in terms of natural regeneration, has been investigated by Gensac (1990), Nakagawa et al. (2003) and Motta et al. (2006). Such importance is crucial in mountain forests where the lack of logs due to exploitation is a noteworthy issue (Nakagawa et al. 2003, Motta et al. 2006); especially though in Central Europe where forests lacking CWD are rather widespread (Kulakowski and Bebi 2004). Considering that the seedling densities on the cut stumps do not differ from natural stumps (from Nakagawa et al. 2001), a better understanding of the role of stumps in the regeneration process in natural spruce forests would enable decision makers to determine differences in the potential of suitable microsites for seedling establishment between natural (with logs) and managed (without logs) forest.

The aims of this study were to analyze the roles of the CWD in the regeneration processes of the two Norway spruce old-growth forests with the special focus on the importance of logs and stumps. The objectives were: 1) to evaluate CWD availability with the emphasis on stump and log identification, 2) to compare the density and height structure of seedlings on logs, stumps and non-CWD microsites with regards to different ground vegetation types.

2 Methods

2.1 Study Site

The first study site is located in Trojmezná, which is situated in southern part of the Bohemian Forest (48°47′N, 13°49′E) in the south-western part of the Czech Republic. Subalpine spruce forests are found between 1150–1450 m a.s.l. in these areas. The altitude of our study plots ranges from 1220 m to 1270 m. The aspect is northern on a gentle slope (to 8°). The total annual precipitation is approximately 1300 mm and the mean annual temperature is approximately 3.5°C (period 1961–2000, Climate Atlas of Czechia). The snow cover reaches up to 2 m. The soils are Leptosols and dystric Cambisols derived from biotitic, coarse-grained granite. Plant communities were classified as *Athyrio alpestris-Piceetum* (Neuhäuslová and Eltsova 2003) with high fern *Athyrium distentifolium* Opiz undergrowth. The old-growth forest (600 ha) where the study site is located has been protected since 1933. At the time of measuring, the canopy closure was mainly 26% on plots (Bače et al. 2009).

The second study site Eustaška is situated in the central part of the Ash Mts. (50°5′N, 17°15′E) in the north-eastern part of the Czech Republic. Subalpine spruce forests are found between 1050–1350 m a.s.l. in these areas. The altitude of the study plots ranges from 1240 to 1270 m. The aspect is south-eastern and the slope is gentle (to 10°). The total annual precipitation in the area is approximately 1300 mm and the mean annual temperature is approximately 3.0°C (period 1961–2000, Climate Atlas of Czechia). The snow cover reaches up to 2 m. The soils are haplic and skeletic Podzols derived from chlorite-sericite phyllite and quartzite. Plant communities were classified as *Calamagrostio villosae-Piceetum* (Banaš et al. 2001) with dwarf shrub *Vaccinium myrtillus* L. undergrowth. The old-growth forest (50 ha) where the study site is located has been protected since 1969. In 1999, the canopy closure was mainly 39% on plots (unpublished data).

Both study sites are believed to be well preserved examples of old-growth spruce forest in the Czech Republic (Natural Forests' Databank… 2004, Svoboda and Pouska 2008). All stands characteristics and high levels of CWD suggest the forests to be old-growth (Janda et al. 2010, unpublished results). The mean age of the tree layer is more than 250 years on Trojmezná (Svoboda et al. 2011). Despite this fact, we have recorded stumps that had been cut on both study sites (Table 1). All these stumps were at advanced decay stages. The historical records describing previous management on both study sites are rather sporadic. Therefore, we believe both study sites were somewhat affected by selective cutting. The study site Eustaška was furthermore affected by grazing (Banaš et al. 2001). The forest on both study sites is dominated by Norway spruce (*Picea abies* (L.) Karst.) with admixture of rowan (*Sorbus aucuparia* L.). Plant nomenclature follows Kubát et al. (2002).

2.2 Data Collection

The two adjacent experimental plots were selected on both study sites. The size of each plot was 1 ha (100×100 m). The experimental plots were selected in places with minimal influence of human activity such as logging or salvage logging in order to prevent CWD removal or the bark peeling.

The research was carried out at the end of growing season 2008. The plots were established using Field-Map (IFER-MMS, Field-Map Technology, 2009, http://www.field-map.com). Field-Map is a comprehensive software and hardware technology for field data collection and subsequent data processing. All stumps of diameter greater than 0.1 m and of length within the range of 0.1 m and 2 m were sampled. The diameter of the stumps was measured at the half-height. All logs with a diameter at the thicker end of the log ≥ 0.1 m and whose length was ≥ 2 m were sampled. The diameters at both ends of logs along with the logs' lengths were measured. The diameters of stumps and their heights were also assessed.

The logs were characterized by their origin (up-rooted living tree, breakage of dead trees with stump (≤ 2 m) or snag (> 2 m), without stump, snag or root-soil plate) and assigned to the recorded stumps. Special attention was paid to the stumps matching other logs found within the experimental plots. Where the fallen stem was broken to the extent that individual parts did not match each other the parts were treated as separate logs. In some cases, more than one log originated from one tree. For instance, forked trees with stem bifurcation below 2 m resulted as one stump with more logs upon falling. The presence of stumps with a flat surface that have likely originated from cutting was also recorded. In order to distinguish between natural and cut stumps, the following categories of stumps were determined: 1) stump with one log, 2) stump with two and more logs, 3) stump without log and without flat surface, 4) stump without log and with a flat surface.

The logs were classified according to the decay stage that was determined according to the degree a knife penetrated the decaying wood. The decay stage classification by Sippola and Renvall (1999) as follows: decay stage 1: recently dead log, wood hard, bark and phloem fresh, knife penetrates only a few mm into the wood; decay stage 2: wood hard, most of the bark left, but no fresh phloem present, knife penetrates 1–2 cm into the wood; decay stage 3, wood partly decayed on the surface or in the centre, usually large pieces of bark loosened, knife penetrates 3–5 cm into the wood; decay stage 4, most of the wood soft throughout, usually no bark present, the whole blade of the knife penetrates easily into the wood; decay stage 5, wood very soft, disintegrates when lifted, log covered by ground-layer mosses and lichens. If the decomposition stage varied in different parts of the log, an average decay stage was recorded.

All individuals of Norway spruce regeneration growing on logs and stumps were recorded and separated into eight different height classes (0–10, 11–30, 31–50, 51–70, 71–90, 91–110, 111–200, >200 cm). Current-year seedlings were excluded because their number changed during the time of the study. In order to determine the correct number of the seedlings growing from the deadwood, only those seedlings with root collar clearly growing from the dead wood were recorded. The age of the tallest individual of natural regeneration on all logs and stumps was estimated. If the log had a root-soil plate where seedlings grew, the age of tallest individual on root-soil plate was also recorded. The age estimation was based on the number of verticils and terminal bud scars visible on the aboveground and eventually underground stem (Zielonka 2006).

To analyze the regeneration patterns (height 0–2 m) on non-CWD microsites, 25 regularly distributed grid sampling sub-plots (5×5 m) were laid out on all experimental plots (total area 625 m^2 per experimental plot). All seedlings growing on all other microsites than on above defined logs and stumps (including buttress, root-soil plates, small woody remains, etc.) were recorded as growing on the non-CWD microsites.

2.3 Data Analysis

We decided to pool the data from the two experimental plots since there were no significant differences in seedling densities on the logs, stumps and non-CWD microsites between the experimental plots on both sites (Mann-Whitney U-test was used).

The Mann-Whitney U-test was used in order to compare between seedling density on CWD and non-CWD microsites. The seedling density of a sample (log, stump, square 5×5 m) was counted as the number of individuals (height 0–2 m) per m^2 of the sample area. The area of logs was calculated as the area of trapezoid and the volume was calculated as the volume of truncated cone. The basal area of stump was calculated from a measured diameter at the half-height. The area of stump (the microsite covered area) was calculated as an area of a circle with the diameter equal to 1.2×measured diameter in order to consider its taper near the ground. The 1.2 factor was derived from the diameter at 0.0 height/diameter at 0.03 height ratio using stem shape of Norway spruce (Šmelko 2000).

Several up-rooted trees (logs without stumps) and the stumps that had been cut (without logs) were recorded on the experimental plots (Table 1). Analysis of densities, ages and height-age relationship of seedlings between logs and stumps were performed on pairs of stumps and the logs they matched. These analysis were performed to avoid the dependency of results on random wind disturbances or artificial logs removal. The stumps with two or more logs were included in these analyses of pairs (separate logs were joined together and considered as one log only).

The Binomial test was used to compare seedling densities between stumps and the logs they matched. Linear regression was applied in order to find out how the seedling density was changing between stumps and logs in relation to log decay stage. The dependence of the stump/log seedling density ratio on the log decay stage was tested. The following formula was used:

$$DR_i = \log\left(\frac{DS_i + 1}{DL_i + 1}\right) \quad (1)$$

where DR_i is density ratio, DS_i is density on stump i and DL_i is density on the log originated from stump i. The Wilcoxon test was used to analyze age differences of the tallest individuals on stumps (root-soil plates) and on original logs (stems). The regression analysis was performed in order to examine the difference of the seedling growth rates (height vs. age) on logs and stumps. We used generalized linear models (Gamma distribution, identity link function) with square root transformation of height measurements. In order to test whether the seedling growth rates differed among microsites we compared the slopes of regression (parallelism test). All statistical analyses were performed using the software R version 2.7.1, available online (http://www.r-project.org).

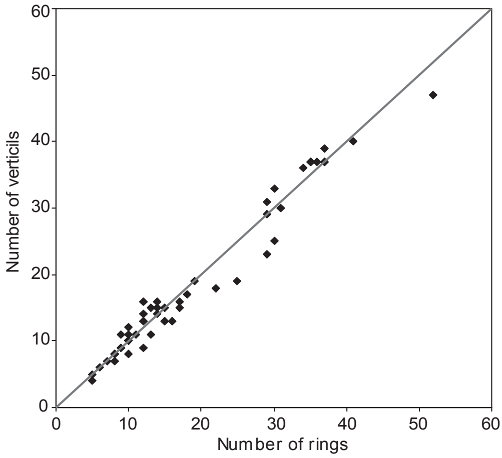

Fig. 1. The relationship between the number of verticils and terminal bud scars on the apical shoot and the number of rings in root collar is represented. The solid line indicates the same values for both methods of the seedling age estimate.

2.4 Verification of Estimated Seedling Age

The estimate of seedling age was verified by closer examination of 70 randomly chosen individuals growing on CWD from wider surroundings of plots. The number of verticils and terminal bud scars visible on leader shoot was counted before the seedlings were excavated. The annual rings at the root collar were counted in the laboratory under the microscope. The number of verticils and bud scars was compared with the number of tree rings of 52 individuals without adventitious roots (Fig. 1). The remaining 18 individuals had

Table 1. Qualitative and quantitative characteristics of coarse woody debris and Norway spruce natural regeneration on the study sites.

	Trojmezná		Eustaška	
	n (ha^{-1})	Mean volume ± SD (m^3)	n (ha^{-1})	Mean volume ± SD (m^3)
LOGS (length≥2.0 m)				
Live tree up-rooted	9.5	3.04±2.12	14.0	1.07±0.80
Snag breakage with stump	40.5	1.80±2.19	54.5	0.86±0.73
Snag breakage with snag	20.5	1.77±2.08	14.5	0.71±0.85
Without stump, snag or root plate	29.5	0.73±1.34	25.0	0.55±0.66
Total	100.0	1.59±2.04	108.0	0.80±0.73
	n (ha^{-1})	Mean basal area ± SD (m^2)	n (ha^{-1})	Mean basal area ± SD (m^2)
STUMPS (height: 0.1–2.0 m)				
With one log	31.5	0.24±0.25	40.5	0.15±0.14
With two and more logs	3.5	0.29±0.18	6.5	0.17±0.14
Without log, without flat surface	23.5	0.20±0.18	16.0	0.12±0.07
Without log, with flat surface	28.5	0.23±0.19	44.5	0.12±0.07
Total	87.0	0.23±0.19	107.5	0.13±0.11
	n (ha^{-1})	Density per microsite (m^{-2})	n (ha^{-1})	Density per microsite (m^{-2})
SEEDLINGS (height: 0–2.0 m)				
On non-CWD microsites	2600	0.27	4300	0.45
On stumps	549	19.61	230	10.97
On logs	2543	5.70	1236	3.75
Total	5700	0.56	5800	0.58

adventitious roots. Estimating the age accord ing to the tree rings is difficult on individuals with adventitious roots (Niklasson 2002, Doi et al. 2008). We believe the age of sampled seedlings with adventitious roots may be slightly underestimated.

3 Results

3.1 Coarse Woody Debris Availability

We recorded 100 (0, 21, 39, 27, 14/decay 1, 2, 3, 4, 5) logs per ha with the mean diameter at larger end 0.44 ± 0.22 m (±SD) with the total volume 159 m^{3}ha^{-1} and the area covering 446 m^{2}ha^{-1} on Trojmezná site. As for Eustaška site, 108 (0,21,41,32,15/decay 1,2,3,4,5) logs per ha with the mean diameter at larger end 0.37 ± 0.13 m with the total volume 86 m^{3}ha^{-1} and the area covering 330 m^{2}ha^{-1} were recorded. Most of the logs recorded originated from the break of dead trees. Such logs matched particular stumps or snags found in the experimental plots. The number of uprooted logs was low but their mean volume was higher compared to other logs on both study sites (Table 1).

Eighty-seven stumps per ha were recorded on Trojmezná site (mean height 0.65 ± 0.39 m, total basal area 19 m^{2}ha^{-1} and covering 28 m^{2}ha^{-1}) as oppose to 108 stumps on Eustaška (mean height 0.53 ± 0.30 m, total basal area 14 m^{2}ha^{-1} and covering 21 m^{2}ha^{-1}). Less than half of the stumps recorded in the experimental plots matched one or more logs. The occurrence of stumps with two and more logs matching was rare. The number of estimated cut stumps was 29 and 46 per hectare with the total basal area being 6.6 m^2 and 5.3 m^2 on Trojmezná and Eustaška respectively (Table 1).

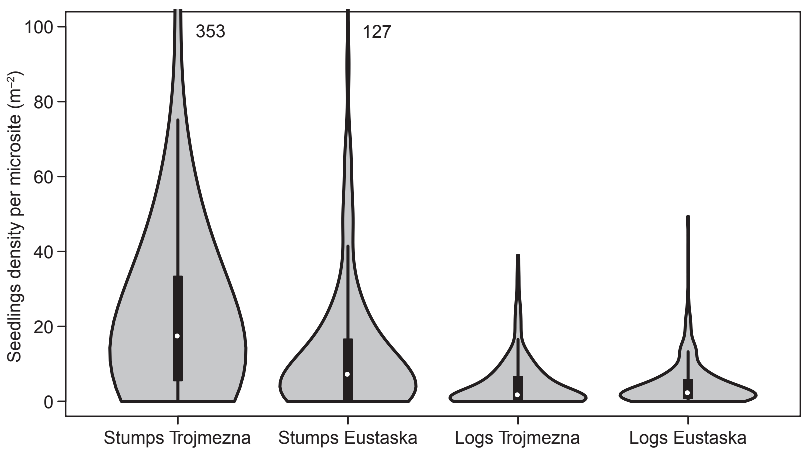

Fig. 2. The distribution of seedling densities per microsite on stumps and logs. A violin plot represents median, 25% and 75% quartiles, range without outliers and kernel density.

3.2 Regeneration Pattern

Spruce seedling density exceeded 5000 ha^{-1} in both study sites. CWD created significantly preferable substrate for natural regeneration compared to non-CWD microsites ($p_{Trojmezná\ (T)}<0.001$, $p_{Eustaška\ (E)}<0.001$). The densities on stumps were roughly three times greater than on logs in both study sites (Table 1). The distribution of seedling density was over-dispersed (Fig. 2). One hundred forty-two out of 173 stumps and 143 out of 215 stumps were occupied at least by one seedling on Trojmezná and Eustaška, respectively. One hundred twenty-eight out of 200 logs and 172 out of 216 logs were occupied at least by one seedling on Trojmezná and Eustaška respectively. The greater number of seedlings growing on stumps and logs (compared to non-CWD microsites) was recorded on Trojmezná study site (Table 1).

The height distribution of seedlings showed a typical "reverse J" distribution on logs and non-CWD microsites (Fig. 3). The height distribution of seedlings on stumps differed since the relative number of seedlings gently decreased with the increasing height class (Fig. 3). Although stumps covered less than 0.3% of ground, one third of seedlings within the height class 111–200 cm were recorded growing on stumps on Trojmezná study site (Fig. 3). The substantial difference in the number of the smallest seedlings between the logs and stumps was present especially on Trojmezná study site, which was caused by the large number of seedlings on logs at decay 3 (Fig. 3). The disproportion between the large number of smaller and low number of taller seedlings decreased with progressing log decay (Fig. 3). Twenty-four seedlings taller than 2 m were found on logs and 88 seedlings of the same height on stumps on Trojmezná site. As for Eustaška site 4 seedlings taller than 2 m were found on logs and 22 on stumps (data not shown).

The seedling densities on stumps were significantly higher than on the logs they matched ($p_T = 0.002$, $p_E = 0.002$, Fig. 4). The number of pairs without seedlings was 3 and 8 on Trojmezná and Eustaška, respectively. The *DR* significantly decreased with increasing log decay stage, considerably more on Eustaška ($R^2_T = 0.10$, $p_T = 0.005$, $R^2_E = 0.17$, $p_E<0.001$). The seedlings were significantly older on stumps than on the original logs ($p_T<0.001$, $p_E<0.001$, Fig. 5). The individuals of the greatest height recorded on the stumps were about 5.1±12.7 (mean ± SD) and 6.2±15.1 years older than ones on the logs they matched on Trojmezná and Eustaška, respectively. The seedlings growing on disintegrating root-soil plates of uprooted trees were significantly older than those growing on their stems ($p_T = 0.001$, $p_E = 0.029$). The individuals of the greatest height recorded on the root-soil plates were about 6.9±6.1 and

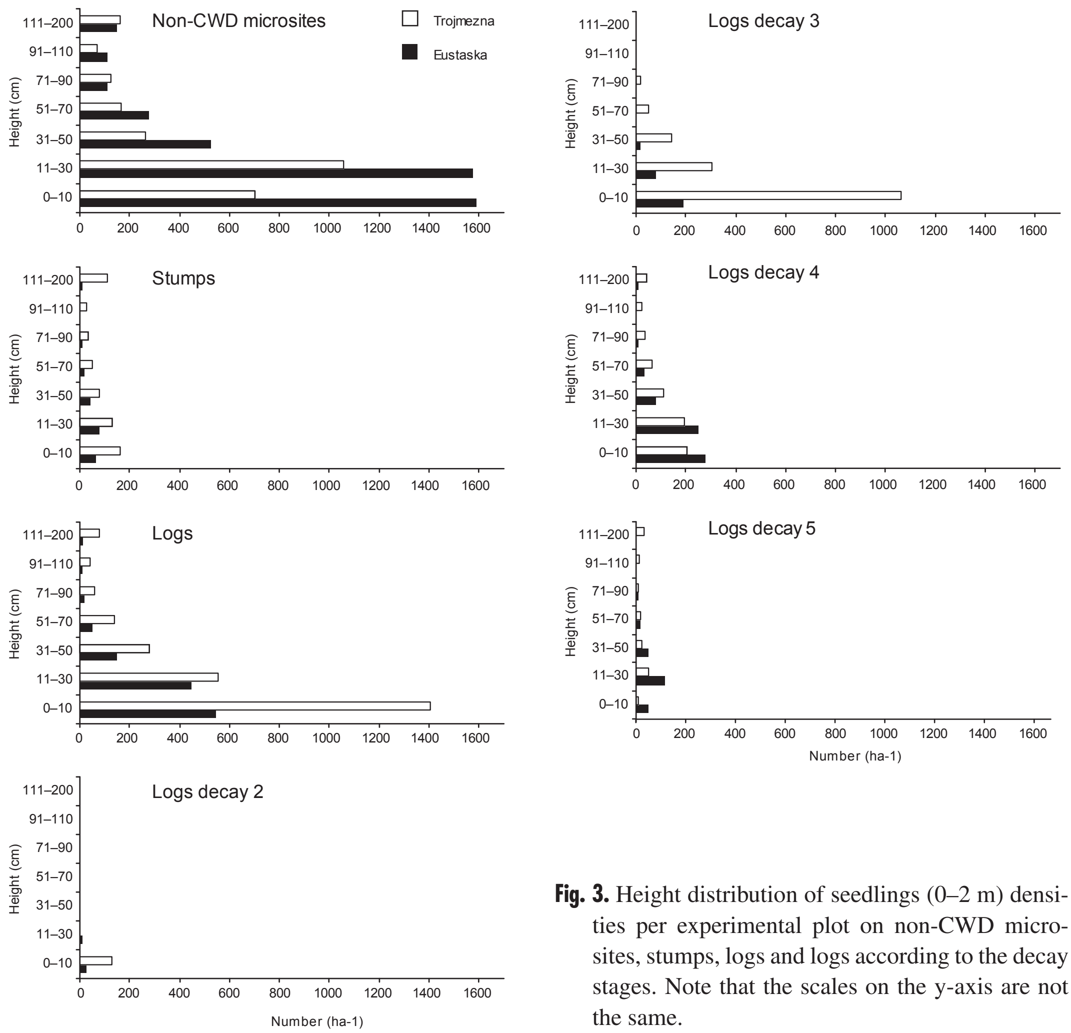

Fig. 3. Height distribution of seedlings (0–2 m) densities per experimental plot on non-CWD microsites, stumps, logs and logs according to the decay stages. Note that the scales on the y-axis are not the same.

4.1±9.4 years older than ones on stems on Trojmezná and Eustaška, respectively. It takes 20 (Trojmezná) and 25 (Eustaška) years for the seedlings growing on both logs and stumps to reach 1.3 m of height as indicated by the regression analysis. The differences in height growth between logs and stumps were not found to be significant ($p_T = 0.087$, $p_E = 0.367$).

4 Discussion

4.1 Regeneration on Stump vs. Regeneration on Log with Regards to Undergrowth Vegetation Type

This study showed that seedling densities are higher on stumps as opposed to logs and non-CWD microsites. Similar to results from Trojmezná (Table 1), the seedling densities 0.2, 5.1 and 19.5 m^{-2} were found in the old-growth spruce forest in altitudinal belt 1260–1360 m in the Western Carpathians on non-CWD microsites, logs and stumps, respectively (calculated from displayed

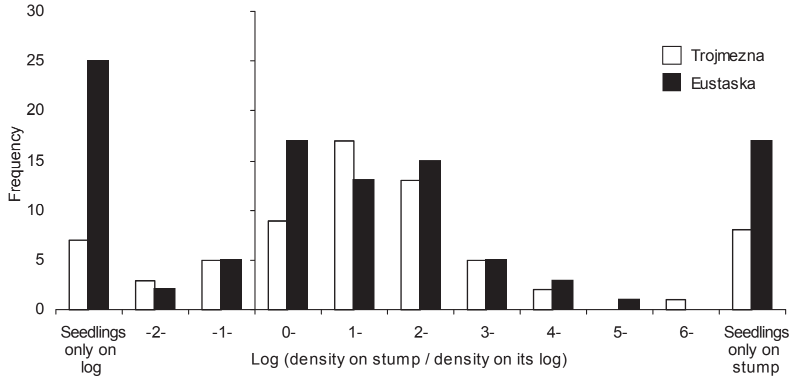

Fig. 4. Frequency histogram where the logarithm of the rate of seedling densities between stumps and the logs they belong to are showed.

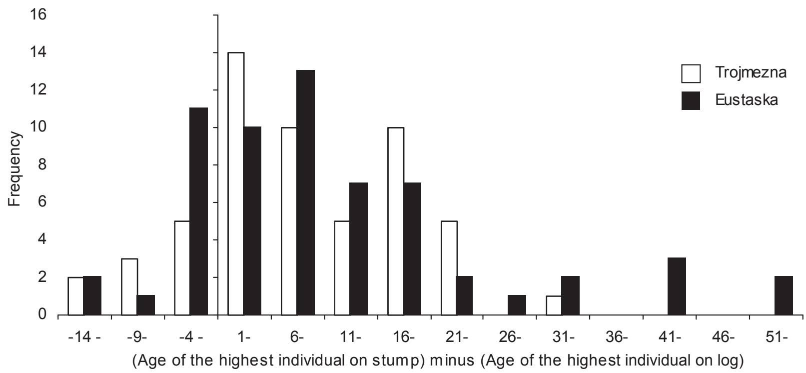

Fig. 5. Frequency histogram where the difference of tallest seedling age between stumps and the logs they belong to is represented. The couples of stumps and the logs they belong to with at least one seedling on both stump and log are showed.

data in paper by Vorčák et al. 2006). Interestingly, the disproportion between the seedling densities on stumps and logs grew with increasing altitude favouring stumps. The seedling densities were six times greater on stumps in the upper belt of subalpine spruce forest in the Western Carpathians (calculated from displayed data in paper by Vorčák et al. 2006). Based on the difference between the ages of the tallest individuals on the stumps and the logs they matched (Fig. 5), stumps (root-soil plates) seemed to provide a favourable seedling microsite several years earlier than the logs (stems). Larger densities of seedlings regenerating on stumps and earlier seedling establishment on stumps rather than on logs can be caused by several factors. Firstly, the stump after the tree breaks immediately creates a suitable substrate for seedling establishment as opposed to log. The rotten part of wood that causes the snag to break, is sufficiently rotten to provide a successful seedling establishment. This is supported by the ascertained decrease of disproportion in seedling densities between the stumps and the logs they match with the log decay progress. Stumps are rooted in the soil, facilitating a faster decomposition process through the transport of nutrients, including nitrogen compounds from the soil, by fungus mycelium (Zimmerman et al. 1995). Furthermore, stumps have more suitable depressions allowing better seed trapping. The seedlings on stump are better protected against ground vegetation competition, not only because of better position above the ground level but also because of their occurrence in different vegetation layers around stumps that is more suitable for seedling establishment (Holeksa 2003, Bače et al. 2009). Additionally, the seedlings could be present on the base of the snag before the tree breaks as well as on the base of a living tree (Takahashi 1994, Sugita and Tani 2001) obtaining nutrients from adjacent soil. In contrast, the seedlings regenerating on top of higher stumps could be subjected to increased mortality due to the disintegration of the stump. On the other hand, the rot in wood proceeds more quickly along the wood fibres (Rypáček 1957) and the roots of seedlings growing on the stumps follow the vertical zones of decaying wood (Narukawa and Yamamoto 2003), which enables the roots of the seedlings to reach the stable soil substrate more readily.

The disproportion in seedling densities between the stumps and the logs they matched decreased with increasing log decay stage less substantially on Trojmezná with *A. distentifolium* undergrowth than on Eustaška with *V. myrtillus* undergrowth. This was likely caused by the advanced decay stages occurring close to the ground level, where the tall forest floor vegetation hindered the establishment of new individuals (Holeksa 2003). This interpretation is also supported by the fact that logs at advanced decay stages in *A. distentifolium* undergrowth were rarely occupied by small seedlings, compared to logs in *V. myrtillus* undergrowth (Fig. 3). Thus, it seems that logs in *A. distentifolium* undergrowth serve as microsite favouring the seedling establishment for a shorter period. In addition, in *A. distentifolium* undergrowth, the stumps have distinctively higher proportion of the taller seedlings compared to the small individuals than the logs and non-CWD microsite (Fig. 3). On the other hand, in *V. myrtillus* undergrowth, stumps and non-CWD microsites have a greater proportion of the taller individuals of natural regeneration compared to the small individuals than logs do (Fig. 3). The findings from Eustaška site were comparable to the study from the same plant association by Kathke and Bruelheide (2010) who concluded that the role of CWD microsites in long-term regeneration has been widely overestimated. According to our results and results from similar studies, this finding is not convincing since the larger portion of taller individuals on CWD compared to the non-CWD was recorded for *P. abies* in subalpine forest of Slovakia (Holeksa et al. 2007) and the Czech Republic (Kotrla et al. 2005, Svoboda et al. 2010) and for *P. glehni* in boreal forest of Hokkaido (Narukawa et al. 2003). In contrast, the taller *P.abies* seedlings dominated on non-CWD microsites compared to CWD in boreal forest of Sweden (Hofgaard 1993) and mixed mountain forests of Poland (Szewczyk and Szwagrzyk 1996). This finding was also reported for *P. jezoensis* (Narukawa et al. 2003), *P. glehnii* (Noguchi and Yoshida 2004), *Tsuga diversifolia* (Sugita and Tani 2001, Narukawa et al. 2003, Sugita and Nagaike 2005) and *T. canadensis* (Krueger and Peterson 2006). Therefore, it is necessary to be cautious when drawing conclusions since the absence of old seedlings on logs can be the result of the logs being removed in the past or by inaccurate determination of microsites in the case of advanced decay of CWD or small woody remnants. Higher densities of seedlings would have been found on CWD on our study sites, especially though on the logs, if some of the logs were not removed in past. As our results indicate, the significance of CWD for *P. abies* seedling establishment is greater in the forest with thick undergrowth since the same findings were reported for conifer species in Japan (Narukawa and Yamamoto 2002, Sugita and Tani 2001, Sugita and Nagaike 2005).

4.2 Links to Forest Dynamics

Our findings suggest that the stumps in natural subalpine spruce forest play (relatively to their covered area or volume) a more important role for seedlings establishment than other microsites. The stumps are relatively evenly distributed in the forest (Svoboda et al. 2010). The early regeneration of spruce seedlings on stumps or root-soil plates increases its competitive advantage. Therefore, they are more likely to grow and successfully reach maturity. Hofgaard (1993) assessed the microsite type for mature trees in the virgin forests of Sweden and found a higher proportion of mature trees growing on stumps in comparison to logs, while the seedlings prevailed on logs.

Numerous individuals of new generation can occur on the same places as the trees of the old stand. The network of lateral tree roots binds soil together while vertical roots anchor the surface layers to the deeper, more stable soil mass (Zhou et al. 1997, Reubens et al. 2007). The limited ability of spruce to establish on microsites that are not raised above the ground level and water-induced soil erosion in treeless patches could influence the forest terrain formation (Reubens et al. 2007). Consequently, permanent depressions can occur in forests and can be occupied by spruce seedlings only if the fall of a large stem facilitates the seedling recruitment. More research across the ecosystems over a long period is needed in order to determine the importance of stumps and logs in forest regeneration.

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