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NORWAY SPRUCE REGENERATION ON DECAYING LOGS IN SUBALPINE FORESTS IN THE TATRA NATIONAL PARK

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Abstract: This study reports temporal patterns of availability of coarse woody debris on the forest floor and its influence on spruce regeneration in subalpine spruce forests in the Tatra Mts. The volume and area of all logs and stumps were measured on four study plots with a total area of 1.432 ha. Spruce regeneration on decaying logs was counted and grouped in age classes. Samples of dead logs were cross-dated to examine the decomposition rate in the climatic conditions of the upper montane belt in the Tatra Mts. On average the total volume of logs was 93 m^3 ha^{-1} and constituted 22% of the stem volume of living trees. Logs and stumps covered 4% of the forest floor, occupying a total of 422 m^2 ha^{-1}. These values are comparable to those of similar natural spruce forests in the Carpathians and Scandinavia. On each studied plot the portions of wood belonging to each of 8 stages were determined; they seem to indicate a fairly constant supply of dead wood to the forest floor, and to confirm the old-growth status of the forest. The oldest cross-dated log came from a spruce tree that stopped growing in 1883. This suggests that the time needed for complete decomposition is relatively high, exceeding 100 years. The best substrate for spruce regeneration consisted in the most decomposed logs (stages 7 and 8), with over 1000 spruce saplings per 100 m^2 log surface. Fresh logs in decay stages 1 to 3 did not provide good conditions for germination and survival of seedlings. Spruce regeneration appears on mid-decomposed logs (stages 4 to 6) about 40 years after tree death.

Key words: *Picea abies,* coarse woody debris (CWD), nurse log, decomposition rate, regeneration pattern, cross-dating, old-growth forest, subalpine spruce forest, Carpathians, Poland

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INTRODUCTION

Coarse woody debris (CWD) is an important part of the forest ecosystem (Harmon *et al.* 1986). Dead wood in woodlands influences a variety of biological, chemical and physical processes. It plays a crucial role in nutrient and water storage (Graham & Cromack 1982; Spies *et al.* 1988). Wood in different decomposition stages provides a habitat for numerous organisms such as bacteria, fungi and invertebrates, which in turn play an important role in nutrient and carbon cycling. Decaying logs, stumps and standing snags host many rare insect, bird and mammal species (Harmon *et al.* 1986). Decaying wood differs from the forest floor and provides specific microsites for plant growth. It is an important substrate for regeneration of tree species. Norway spruce *Picea abies* (L.) Karst. is one of several tree species whose regeneration is strongly related to decomposed wood. The importance of dead wood as a regeneration substrate has been reported from many mountain forests in the Austrian Alps (Mayer *et al.* 1972) as well as the Carpathians (Korpel 1989; Jaworski & Karczmarski 1989; Holeksa & Ciapała 1998). Spruce regeneration on nurse logs is also well known from the boreal forests of Scandinavia (Hytteborn & Packham 1987; Hofgaard 1993; Kuuluvainen 1994; Hörnberg *et al.* 1995). Probably one advantage of dead wood substrate is that it provides favorable microclimatic conditions and isolates saplings from the competition of ground vegetation (Sollins *et al.* 1987; Harmon & Franklin 1989). However, there are still few quantitative studies on the preferences of spruce for regeneration on specific wood decomposition stages (Holeksa 1998).

Here we report the frequencies of occurrence of spruce saplings and the decomposition stages of decaying logs in natural subalpine forests of the Tatra Mts. In a preliminary study we attempted to estimate when the wood on the forest floor becomes a suitable substrate for spruce regeneration. We believe that deeper insight into the dynamics of CWD and the regeneration pattern in old-growth forest will help conservationists to mimic natural mechanisms in managed forest.

MATERIAL AND METHODS

STUDY AREA

The study was conducted in the Tatra National Park, in the highest part of the Polish Carpathian Mts. The study area is located in the upper montane belt at alt. 1200–1450 m (19°40'E, 49°10'N). The climate is cool and moderately wet. Annual precipitation is high and reaches 1800 mm yr^{-1}. The average annual temperature is 2–4°C (Hess 1996). Common soils of the area are acid podzols formed on granite bedrock. (Komornicki & Skiba 1996). In the Western Tatras where one plot was established (Dolina Pyszna valley) it overlies metamorphic bedrock (Klimaszewski 1996). The field layer vegetation is dominated by *Vaccinium myrtillus* L., *V. vitis-idea* L., *Lycopodium annotinum* L., *Hupertzia selago* (L.) Bernth. *ex* Schrank & Mart., *Listera cordata* (L.) R. Br., *Sphagnum girgensonii* Russ and *Polytrichastrum formosum* Hedw. From a phytosociological view the forest represents the *Plagiothecio-Piceetum* association and is dominated by Norway spruce. Single individuals of stone pine *Pinus cembra* L., dwarf pine *Pinus mugho* L. and larch *Larix decidua* L. are found occasionally on steep slopes outside the studied plots. In gaps and thinned spruce stands, abundant rowan *Sorbus aucuparia* L. regeneration often occurs. The studied stands are uneven-aged; some of the oldest spruce trees are 350 years old (Zielonka 1996). The studied forest has not been managed for at least several decades. Due to the inaccessibility of the steep rocky slopes it is likely that direct human impacts were relatively slight in the past.

FIELD MEASUREMENTS

Four rectangular plots of 0.3–0.5 ha were chosen in the best-preserved old-growth forest stands (Table 1). The plots were established in areas with the least evidence of human activity, with no signs of tree harvest, so that the natural structure of coarse woody debris could be studied. Each plot was laid out to include a homogenous patch of the stand. The sampled area comprised 1.423 ha in total. Within the plots the diameter at breast height (DBH) of all living and dead standing trees (DBH > 10 cm) and the height of *ca* 20% of the trees representing different DBH classes were recorded. The length and diameter at both ends of each log thicker than 10 cm at the larger end were measured. The base diameter and height of stumps were recorded. Stages of decomposition of dead wood were described using Holeksa's (1998) 8-degree scale, slightly modified (Table 2). Spruce seedlings and saplings growing on each log were counted. We determined the approximate age of each sapling by counting verticils (Sirén 1951; Chojnacki 1964), and grouped them in 5-year classes. In a preliminary study near one plot (Dolina Roztoka valley), increment cores were taken from 20 living dominant trees, and 20 cross-section samples were cut from logs representing different decay stages to determine the time since tree death.

CALCULATIONS AND CROSS-DATING

The stem volume of live and dead standing trees were calculated using empirical tables of standing tree volume. Log volumes were calculated using the formula for a truncated cone:

$$(1)\ V\ (m^3) = \pi / 12 \times L\ (D_{max}^2 + D_{max} \times D_{min} + D_{min}^2),$$

where L is log length, and D_{max} and D_{min} are maximum and minimum log diameter. This approach might underestimate the volume of logs slightly. The orthogonal projections of logs on the ground were calculated

Table. 1. Characteristics of plots.

Location	Altitude (m)	Exposure	Area (ha)	Inclination (°)
Dolina Roztoka valley	1200	N	0.425	0
Czuba Roztocka Mt.	1400	N	0.281	30
Dolina Waksmundzka valley	1300	SE	0.300	5
Dolina Pyszna valley	1420	NE	0.417	22

Table. 2. CWD decomposition scale (after Holeksa 1998, slightly modified).

Stage of decom- position	Shape	Depth of penetration of knife	Branches	Bark
1	round, smooth	wood hard	all branches present	intact
2	round, smooth	surface bends under pressure of knife	branches over 2 cm thick present	partially intact
3	round, furrows, several mm deep	to 1 cm	over 3 cm thick present	remains on upper side of log
4	round, furrows, *ca.* 0.5 mm deep	to 4 cm	only base part present	usually lack
5	round, furrows *ca.* 1 cm deep	to 5 cm	only thickest base parts present	lack
6	slightly flattened, several cm thick pieces tear off	solid only in central part of log	only thickest base parts present	lack of any remains
7	distinctly flattened, whole log covered with furrows several cm deep	through	lack of any remains	lack of any remains
8	flattened, covered with vegetation	through	lack of any remains	lack of any remains

using the formula for the area of a trapezoid. To determine the year of death of trees representing different stages of decomposition, the classical 'cross-dating on the wood' method was used (Douglass 1941; Stokes & Smiley 1968). Tree-ring patterns of cross-sections extracted from decayed logs were compared with the growth trend of living trees. As pointer years we used specific narrow rings as well as the abnormal earlywood to latewood ratio (Schweingruber *et al.* 1990). With this approach the ages of logs – the time since tree death – were determined. In the samples where the last-formed ring was present under the bark, it was possible to determine the exact year of tree death. The minimum age of logs too decayed to be cross-dated was estimated from the highest age of spruce saplings growing on the log (Sollins *et al.* 1987; Dynesius & Jonsson 1991).

Because all plots presented similar conditions that could influence regeneration processes on the dead wood (e.g., light conditions), the data collected in the plots was combined in one sample to analyze the regeneration pattern of spruce. We used the chi-square test to determine whether the density of spruce regeneration growing on the logs depends on the decay stage of the wood. We used the nonparametric Kolmogorov-Smirnov two-sample test to check whether the distributions of age classes of regeneration differed between substrates (decay stages 4 to 8).

RESULTS

STAND STRUCTURE

The mean volume of the living trees was 426 m^3 ha^{-1} and the average number of living stems (DBH ≥ 10) was 351 per ha. The larger number of trees in the thicker-diameter classes in the Dolina Waksmundzka and Dolina Pyszna valleys (Fig. 1) is reflected in the higher living stand volume in these plots (Table 3). The lower volume of living trees in the Dolina Roztoka valley and on Czuba Roztocka Mt. was compensated by the higher volume of standing snags in these plots (Table 3). In the studied forests we recorded 140 standing dead trees per ha on average; the volume of snags averaged 113 m^3 ha^{-1}, and varied between plots from 64 to 186 m^3 ha^{-1}.

ABUNDANCE OF COARSE WOODY DEBRIS

In the studied area the mean density of logs and stumps was 201 units per ha. The total mean volume of downed logs was 93 m^3 ha^{-1} and varied between plots (Fig. 2). CWD constituted 22% of the volume of living trees. Because the volume of

Table. 3. Characteristics of living and dead trees by volume and number.

Plot	Living trees		Standing snags		Logs		Living and dead wood
	Volume (m^3 ha^{-1})	Density (no. ha^{-1})	Volume (m^3 ha^{-1})	Density (no. ha^{-1})	Volume (m^3 ha^{-1})	Density (no. ha^{-1})	Volume (m^3 ha^{-1})
Dolina Roztoka val.	331	412	113	118	87	249	531
Czuba Roztocka Mt.	278	332	186	199	108	194	572
Dolina Waksmundzka val.	613	382	89	176	113	259	815
Dolina Pyszna val.	481	290	64	69	64	103	609
Average	426	351	113	140	93	201	632

stumps was low (6 m^3 ha^{-1}), they were included in the log category. Figure 2 shows the portions of wood in different stages of decay on each plot (Fig. 2). On some plots (Dolina Roztoka valley and Czuba Roztocka Mt.) the distribution of decay stages is fairly even. The distribution is skewed towards the fresher stages of decomposition only on the Dolina Waksmundzka valley plot. On all plots the volume of the more decomposed classes (7 and 8) was lower. The average volume and number of logs for all plots were relatively equal between different decay classes (Fig. 3).

The mean diameter of logs was 0.39 (S.D. = 0.13) for decay stage 1, and as follows for the other decay stages: 2 – 0.27 (0.15); 3 – 0.28 (0.14); 4 – 0.31 (0.13); 5 – 0.33 (0.14); 6 – 0.35 (0.13); 7 – 0.33 (0.12); 8 – 0.30 (0.07). The number of thick logs decreased with advancing decay stages. Logs thicker than 0.4 m constituted 26% of the fresher logs (decay stages 1–3) and 14% of the medium-decomposed logs (decay stages 4–6). Although the mean diameter of the most decomposed logs in decay class 7 and 8 did not differ considerably from the other classes, only 9% of these most decayed logs exceeded 0.4 m in diameter. Downed logs and stumps covered over 4% of the forest floor, occupying 422 m^2 ha^{-1}.

Successful cross-dating was possible for only 10 logs belonging to decay stages 1 to 5 (Table 3). More decomposed logs could not be dated because they were too eroded to produce a clear profile of tree rings. The oldest cross-dated log came from a spruce tree that stopped growing in 1883. Due to the small sample size the results of the cross-dating procedure must be treated as tentative. The age of the oldest spruce growing on a log in decay stage 8 was estimated at 70 years. Correspondingly younger spruces grew on the less decomposed logs (Table 4).

Table 4. Estimation of log ages by cross-dating and by age of existing regeneration.

Stage of decomposition	Years since tree death obtained from	
	cross-dating	oldest regeneration
1	< 4	–
2 + 3	8 – 43	14
4 + 5	44–115	40
6 + 7	–	40
8	–	70

REGENERATION PATTERN

On the total area of 567 m^2 covered by CWD, 1975 spruce saplings from 3 to 70 years old were found. No 1-year-old seedlings were noted on the decaying wood. The first three decomposition stages do not provide suitable conditions for spruce regeneration; only 36 saplings were recorded on 106 logs in those stages, and the age of the oldest spruces did not exceed 14 years (Table 4). Spruce

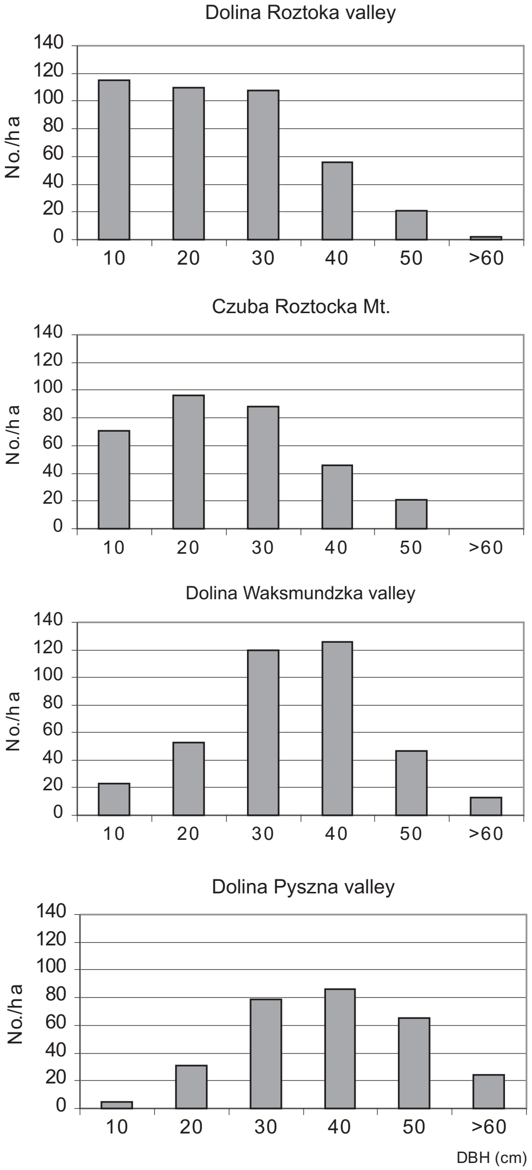

Fig. 1. Diameter class distribution for living trees on 4 plots.

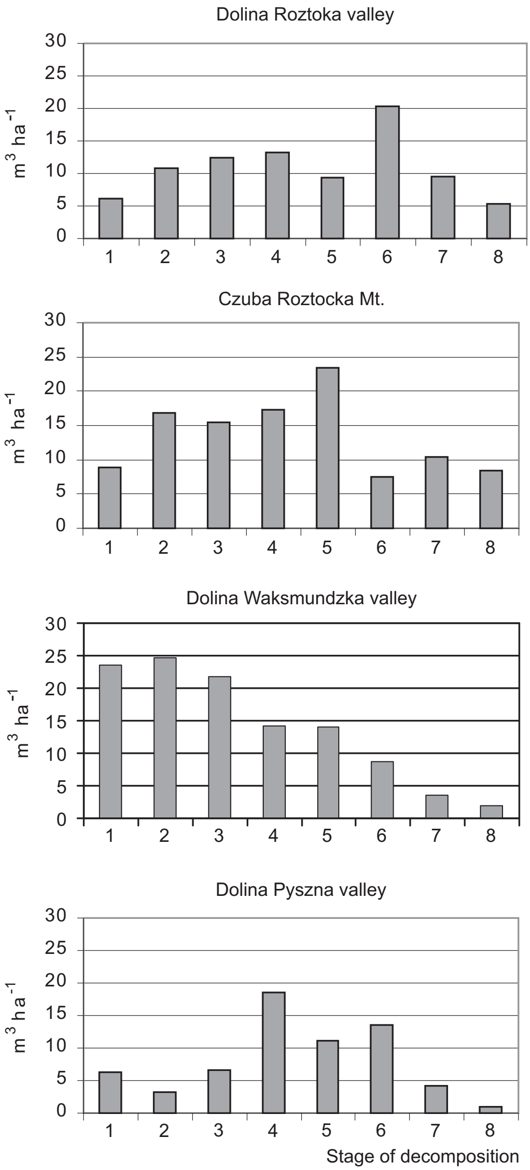

Fig. 2. Volume of CWD for 4 plots, by decay stage.

saplings were more abundant beginning with decay stage 4. The highest number of young spruce trees was observed on logs in decay classes 7 and 8, constituting 60% of all individuals observed on logs. On the most decomposed logs their density exceeded 1000 individuals per 100 m^2 (Fig. 4). The distribution of spruce regeneration depended on the stage of decomposition of the wood ($\chi^2 = 1929$; df = 7; $p < 0.001$). The distribution of sapling density versus log diameter is given in Fig. 6. The highest density of saplings was on logs 20–49 cm in diameter.

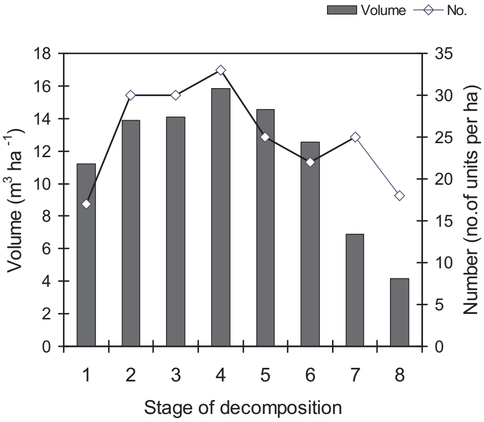

Fig. 3. Total volume of logs for all plots combined.

The age structure of saplings was similar for logs in all decay stages and resembled a reverse J curve. Saplings aged 14 years and younger constituted over 88% of all individuals growing on the logs. Regardless of log decay stage, young saplings of the first three age classes were always the most numerous. The density of older age classes of regeneration increased only slightly with advancing decay stages (Fig. 5). The distributions of age classes of spruce saplings growing on logs in decay stages 4 to 7 did not differ significantly (nonparametric Kolmogorov-Smirnov two-sample test; $p > 0.05$). The distribution of age classes of regeneration on the most decom-

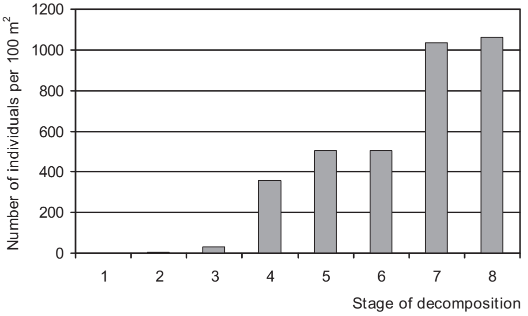

Fig. 4. Density of saplings growing on logs in different stages of decay.

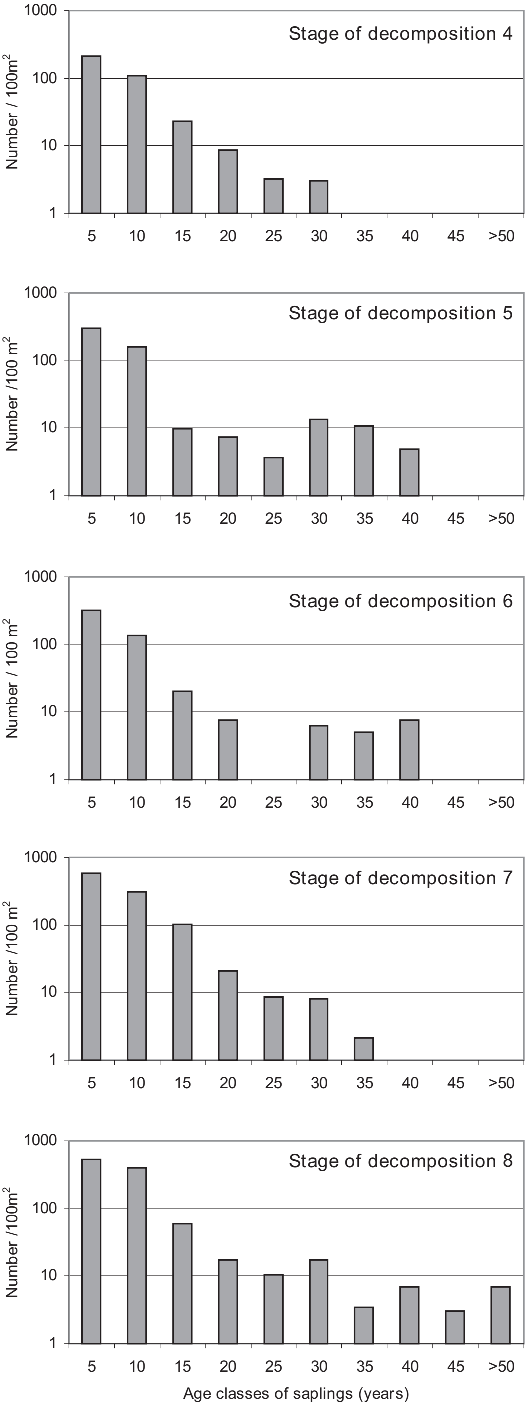

Fig. 5. Spruce regeneration on dead logs in different stages of decay.

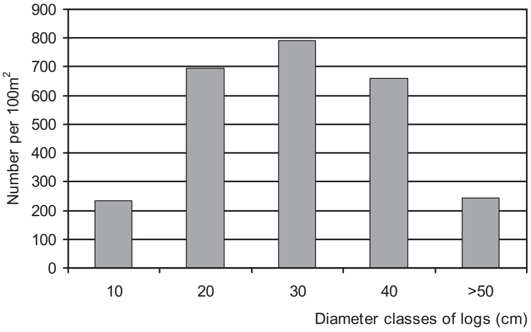

Fig. 6. Density of spruce saplings on logs in different diameter classes, calculated for decay stages 4 to 8.

posed logs in stage 8 differed from the distribution in the other stages.

DISCUSSION

The total volume of fallen logs (93 m^3 ha^{-1}) is in accordance with other observations from natural spruce forests. In the nearest studied forest of the same type and climatic conditions in Babia Góra, Holeksa (1998) measured similar volumes of logs (73 m^3 ha^{-1}), and the volume of the living trees was 407 m^3 ha^{-1}. In the Ural taiga the mean volume of decaying logs examined by Kuuluvainen *et al.* (1998) was somewhat higher (117 m^3 ha^{-1}). The volume of dead wood measured near the timberline in Finland varied from 20 to 60 m^3 ha^{-1} (Sippola *et al.* 1998), and in Swedish virgin spruce forests it was estimated at 58–201 m^3 ha^{-1} (Linder & Östlund 1992; Linder *et al.* 1997).

The total volume of wood accumulated in the form of living stems, snags and fallen logs varied little between plots. In the Dolina Roztoka valley, Dolina Pyszna valley and at Czuba Roztocka Mt. the total wood biomass contained in living and dead stems varied considerably less (531–609 m^3 ha^{-1}) than the volume of living trees (278–481 m^3 ha^{-1}), snags (64–186 m^3 ha^{-1}) and logs (64–108 m^3 ha^{-1}) (Table 3). The volumes of living stems, snags and logs in the studied plots balanced each other out to some extent. This clearly indicates that the volume of logs in the forest should be considered in relation to stand characteristics such as other forms of dead wood and the volume of living trees.

Logs in all decay stages were present even on the small scale of a single plot (Fig. 2). The distribution of logs between decay stages was fairly even, especially on the Dolina Roztoka valley and Czuba Roztocka Mt. plots. Only in the Dolina Waksmundzka valley plot were logs in fresher stages of decomposition dominant, but more-decayed logs were still present. The volume of logs in the most decomposed stages (7 and 8) observed on all plots was lower because thick outer pieces of wood fell off (Table 2). Moreover, the most rotten logs adhere to the ground entirely, making it difficult to distinguish them from the forest floor. This may suggest steady supply of dead wood to the forest floor, even at the relatively small scale. Tree mortality occurs primarily as the death of single trees or small groups of trees.

The stage of log decomposition has a great influence on spruce regeneration. Logs in the initial stage of decay are too fresh and the wood still too hard for successful establishment of seedlings. Downed stems usually lose their bark quickly, and their smooth surface hinders deposition of seeds, which slide off. Wood tissue is too compact to be penetrated by seedling roots. The first intensive appearance of spruce saplings takes place on medium-decomposed logs classified stage 4 at least. The eroded surface of medium-decomposed logs covered with cracks and furrows is more likely to retain seeds. Beginning with decay stage 4 there is successive improvement of conditions for germination and growth of young individuals. The exterior of these logs consists of soft wood which can be penetrated by roots easily. Decaying logs usually are distinguished by increased moisture, and saplings can be supplied with water even during dryer periods (Sollins *et al.* 1987). Contact of the log with mineral soil increases in decay stage 4; this may lead to penetration of the wood by mycelia and thereby improve the supply of biogens (Wells & Body 1995). The most decomposed wood (stages 7 and 8) was the best substrate for young spruces, as indicated by the high density of saplings. The most decomposed logs are usually covered with a dense layer of herbs and mosses, but that does not seem to limit germination processes and growth much. Some vascular species like *Vaccinium myrtillus* or layers of *bryophytes* may smother spruce saplings (Hörnberg *et al.* 1997). On the other hand, the presence of liverworts may influence mycorrhizal interaction with spruce regeneration (Amaranthus *et al.* 1994). The presence of the youngest age classes of saplings on logs in each of decay stages 4 to 8 shows that germination takes place continuously regardless to the wood's decomposition stage. The distributions of age classes of spruce regeneration do not differ between decay stages 4 to 7, indicating similar patterns of colonization on these logs. The higher density of older regeneration on the most decayed logs (stage 8) shows that wood in the terminal stage of decomposition may incorporate ten-year-old spruce regeneration into the field layer of the forest after its complete disappearance.

A study of the influence of log diameter on the density of regeneration confirms that thinner boles (< 20 cm) make a small contribution to spruce regeneration (Holeksa 1998). The most important for regeneration seem to be logs between 20 and 49 cm in diameter. In the Babia Góra forest, Holeksa (1998) noted that the most favorable conditions for sapling growth were provided by logs of the largest diameter, especially those over 50 cm. In this study in the Tatra Mts the number of thick logs in the most decomposed stages was relatively low. For example, in the most decomposed class of logs (8), where spruce regeneration was the most abundant, no log was more than 40 cm in diameter. Only 15% of the logs more than 50 cm in diameter were in decay stage 7. This helps explain the lower density of saplings on logs over 50 cm in diameter (Fig. 6). The good conditions for sapling growth on thick logs are probably related to increased light on an uplifted object and to separation from ground vegetation. Probably when the log is thicker than 50 cm this effect is enhanced, according to observations from Babia Góra Mt.

Dead wood is a selective substrate. No other tree species beside spruce was observed on decaying wood, despite the high abundance of rowan saplings growing in the mineral soil locally on some plots.

Spruce wood is relatively soft and does not form heartwood, so it may decompose faster than wood of many other coniferous species. Rapid decomposition of spruce logs has been reported from southern Scandinavia. Hytteborn and Packham (1987) estimated that 50–70 years is required for complete decomposition of spruce logs. The harsh climate of northern forests may extend this time up to 200 (Hofgaard 1993), or even 300 years (Arnborg 1942). At Babia Góra Mt., with climate similar to that of our plots, Holeksa (1998) estimated the maximum time of decomposition at 160 years. The age of logs from the most decomposed stage (8) was at least 70 years, as estimated by the age of spruces growing on the log. Young spruces usually grow very slowly on logs (Hyteborn & Packham 1987) and sometimes do not produce growth rings or show distinct shoot growth. Thus the number of verticils reflects rather the minimum age. To obtain the correct age of a log it is necessary to add the lag between tree death and the establishment of regeneration. Since the age of logs on which more abundant regeneration occurred (decay stages 4 and 5) (Fig. 3) was cross-dated at 44–100 years (Table 3), this preparatory period may take around 50 years (Hofgaard 1993). Thus, decay classes 7 and 8 are probably obtained 90–110 years after tree death (Table 4).

According to preliminary estimations of log ages, decay stage 4 is reached at least 40 years after tree death (Table 4). At Babia Góra Mt. this stage of decay was estimated at 32 to 57 years after tree death (Holeksa 1998). Thus, logs provide conditions for germination and successful growth only about 40 years after tree death. This study confirms that spruce wood in the subalpine forests of Carpathians decomposes relatively slowly, and it may take over 100 years for a downed log to disappear from the forest floor.

The high volume and relatively equal distribution of decay stages confirms the old-growth status of the studied forest. The best substrate for spruce regeneration seems to be well-decomposed logs, but continuous availability of decay stages is necessary to provide suitable microsites in the future. To improve natural regeneration in Carpathian subalpine forests it would be advisable to maintain the natural structure of coarse woody debris on the forest floor. The high volume of dead wood now accumulated in the form of standing snags probably will become a new substrate for spruce regeneration in the Tatra forests in a few decades. Cross-dating of dead wood, a little-used method at present, is a promising way of better understanding the dynamics of coarse woody debris.

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