Journal of Vegetation Science 17: 739-746, 2006

When does dead wood turn into a substrate for spruce replacement?

Zielonka, Tomasz

Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland;
E-mail tomasz.zielonka@ib-pan.krakow.pl

Abstract

Question: How many years must elapse for freshly fallen *Picea abies* stems to be transformed into a substrate for *P. abies* recruitment?

Location: Natural sub-alpine spruce forest, 1200-1300 m a.s.l., western Carpathians, Poland.

Methods: Coarse woody debris (CWD) was measured on nine plots with a total area of 4.3 ha. All individuals of *P. abies* regeneration growing on dead wood were counted and their age was estimated. Decay rate of logs was determined using dendrochronological cross-dating of samples from logs in different decay stages.

Results: Although CWD covered only 4% of the forest floor, 43% of the saplings were growing on decaying logs and stumps. The highest abundance of *P. abies* recruitment occurs on logs 30-60 years after tree death, when wood is in decay stages no. 4-7 (on an 8 degree decay scale). However, much earlier colonization is possible. The first seedlings may germinate on a log during the second decade after tree death and survive for decades. Their slow growth is possibly due to the gradual progressive decomposition of wood.

Conclusions: This study confirms the importance of decaying wood for *P. abies* recruitment. The decaying logs exhibit continuous and favourable conditions for the germination of *P. abies* seeds throughout their decay process. Logs, irrespective of their decay stage and age, are colonized by young seedlings. This recruitment bank is constantly renewed.

Keywords: Age structure; Dendrochronology; Regeneration pattern; Residence time; Spruce; Sub-alpine forest.

Abbreviation: CWD = Coarse woody debris.

Introduction

The regeneration of tree species on decaying wood has been observed in a wide spectrum of species and geographical regions (Harmon et al. 1986). *Picea abies* (Norway spruce) exhibits this relationship as its natural regeneration is closely related to the presence of coarse woody debris (CWD). The importance of this substrate was confirmed in alpine and Carpathian forests (Mayer et al. 1972; Korpel 1989; Jaworski & Kaczmarski 1989; Holeksa 1998; Zielonka & Piątek 2004) as well as in the boreal forests of Fenno-Scandia (Hytteborn & Packham 1987; Hofgaard 1993; Kuuluvainen 1994; Hörnberg et al. 1995).

Researchers usually link the abundant occurrence of *P. abies* recruitment on decaying logs to the formation of specific microhabitats and the isolation of saplings from competition with plants on the forest floor (Sollins et al. 1987; Harmon & Franklin 1989). The decay process alters the physical and chemical features of CWD as a substrate for seedlings. For example, nitrogen content increases with decay (Hendrickson 1991; Zimmerman et al. 1995). Decaying wood is usually characterized by higher water capacity than that of mineral soil. Dead wood also provides favourable conditions for mycorrhizal fungi that may promote the growth of seedlings.

However, little is known about the course of CWD colonization in time and there are few well documented data concerning the decay rate of logs (Kruys et al. 2002). Time needed for complete decomposition has only been roughly estimated by some authors (Liu & Hytteborn 1991; Hofgaard 1993; Næsset 1999). Wood decomposition and its influence on colonization could be directly studied through long-term observation. However, such analyses are difficult because of the lack of permanent study plots. One alternative to direct observation is reconstruction of the decay rate and history of colonization through dendrochronolocial cross-dating.

In this study, I determined the time needed for *P. abies* logs to be transformed into a substrate for the germination and growth of *P. abies* seedlings in sub-alpine conditions using cross-dating of CWD.

Methods

Study site

The study was conducted in the sub-alpine forests of the Babia Góra Mts. and the Tatra Mts. Both massifs belong to the highest ridges in the Polish Carpathians and are ca. 35 km apart. The sub-alpine *P. abies* forests cover the mountain slopes between 1200 and 1550 m a.s.l. in the Tatras and those at 1150-1390 m a.s.l. on Babia Góra. Within these altitudinal belts, mean annual temperature ranges from 2.5 °C to 4 °C and annual precipitation from 1400 to 1800 mm (Hess 1996). In the Babia Góra massif the soils are mainly orthic podzols and cambisols developed from Magurian sandstone with mudstone interbeddings (Adamczyk & Baran 1963). In the Tatra Mts. similar soils, but with more podzolic rankers umbric leptosols and even lithic leptosols, occur over granites and metamorphic rocks (Komornicki & Skiba 1996).

Sub-alpine *P. abies* forests in both massifs are representative of the acidophilous *Plagiothecio-Piceetum* (Matuszkiewicz 2001). Some of the oldest *P. abies* reach 350 years old (as measured at breast height (Zielonka 1996). A mixture of other trees may also be present, including *Sorbus aucuparia, Larix decidua, Pinus cembra* and *Betula pubescens* ssp. *carpatica*. In the study plots mean density of trees (DBH ≥ 10 cm) was 314/ha and mean volume 454 m^3/ha. The mean density of dead standing trees was 101/ha which were mostly in thinner diameter classes. In the shrub layer, *P. abies* and *S. aucuparia* saplings dominate, as well as *Ribes petreum* and *Lonicera nigra*. The ground vegetation is dominated by: *Vaccinium myrtillus, Athyrium distentifolium, Deschampsia flexuosa, Oxalis acetosella, Dryopteris dilatata, Homogyne alpina* and *Luzula sylvatica* (Kasprowicz 1996).

The forests studied belong to the best preserved sub-alpine forests in the western Carpathians. Both areas have been protected since 1954 as the Tatra and Babia Góra National Parks. The absence of intensive management, coupled with the presence of dead wood and the natural structure of the stands, were the main reasons for choosing this area as the study site.

Data collection

Four plots were established in the Tatra Mts. and five in the Babia Góra Mts. Square or rectangular plots were established in homogeneous fragments of the old-growth forest, characterized by a similar structure and lack of discontinuity within the plot caused by the terrain. The size of the plots varied between 0.2-0.7 ha. The total area of plots was 4.3 ha. The forests in the selected plots were free from visual signs of human activity such as cut stumps or mechanical abrasion of standing trees. Additionally, most of the plots were located in remote sites that are difficult to access. This resulted in a relatively high amount of downed wood that has not been removed for several decades.

Within the plots, all CWD units in the form of logs were measured to calculate the area of projection using the formula for area of a trapezoid. All sections of lying dead wood longer than 1 m and with a diameter of > 10 cm were treated as CWD. For each log, the length and the diameter of both ends were measured. The decay stages of CWD units were identified according to the eight degree scale (slightly modified after Holeksa 1998) (Table 1).

In 2001, all individuals of *P. abies* growing on CWD were counted and their age was estimated. The age estimation was based on the number of verticils and node scars visible on the leader shoot (Niklasson 2002).

Table 1. Characteristics of logs in different decay stages (modified after Holeksa 1998).

Stage of decomposition	Surface	Shape	Depth of penetration of knife	Branches	Bark
1	Smooth	Round	Wood hard	All branches present, elevated above ground	Intact
2	Smooth	Round	Surface bends under the pressure of knife	Branches over 2 cm	Partial intact
3	Crevices several mm deep	Round	To 1 cm	Over 3 cm thick present	Remains on upper side of log
4	Crevices ca. 0.5 mm deep	Round,	To 4 cm	Only base part present	Usually lack
5	Crevices ca. 1 cm deep	Round,	To 5 cm	Only thickest base parts present	Lack
6	Several cm thick pieces tear off	Slightly flattened	Solid only in central part of log	Only thickest base parts present	Lack of any remains
7	Whole log cover with several cm deep furrows	Distinctly flattened	Through	Lack of any remains	Lack of any remains
8	Most often covered with vegetation	Flattened, covered with vegetation	Through	Lack of any remains	Lack of any remains

This method is very simple and enables easy estimation for a large number of seedlings without destructive sampling. To calibrate the method, 15 individuals with a different number of verticils were chosen randomly and cut at the base. The number of verticils was then compared with the number of tree rings at the root collar. Problems connected with precise determination of the age of seedlings – discussed by DesRochers & Gagnon (1997) and Niklasson (2002) – were taken into consideration. In the results, seedlings were grouped in age classes with five year intervals. At least the first three of these age classes consisted of cohorts germinated following three mast years. To avoid the problem of inaccuracy for the estimation of the age of older seedlings, seedlings 45 years old and older were placed in a single age class.

The density of seedlings growing on CWD and on mineral soil was compared. Circular plots (radius 1.5 m) were established in a network of 10 m × 10 m squares in each study plot and seedlings on mineral soil were counted. If CWD was present within the circle, the plot was excluded. The number of subplots varied from 16 to 54 depending on the area of plot, and their pooled area approximated with the area of projection of CWD.

To determine the age of logs, cross-dating was applied (Dynesius & Jonsson 1991). The number of years elapsed since tree death was regarded as log age. Cross sections of wood were extracted from randomly chosen logs representing different stages of decay. The point of sampling of the log was carefully chosen to obtain wedges with the best preserved outer part of the bole, possibly with bark remains. The samples were then dried and polished with a belt sander. The width of rings was measured with the LINTAB measuring table and TSAP software (Rinn 1996). Reference chronology was constructed separately for the Tatra Mts. and Babia Góra Mt. using cores from 20 living trees for each area. Each tree was cored twice in perpendicular directions and the mean measurement obtained. The cores, similarly to the cross sections of dead logs, were dried and measured. The accuracy of the measurements was checked by COFECHA using the correlations of 25 year long sections. Time series were indexed with a 5-point running mean, this method was chosen because of its simplicity (Baillie & Pilcher 1973). A series of samples was then compared with the chronologies to identify the calendar year of tree death, the cross-dating results were also controlled using pointer years (Schweingruber 1989).

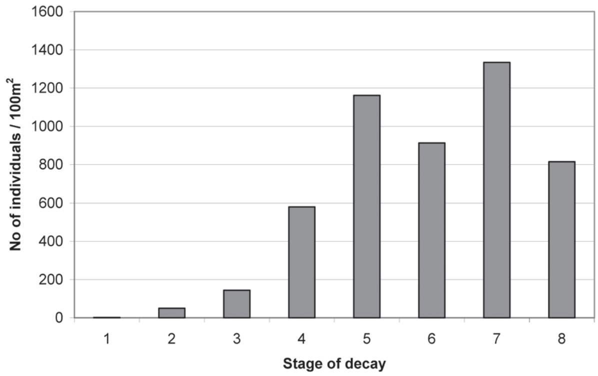

Fig. 1. The density of seedlings growing on dead logs. Mean values for all plots shown.

Results

There were 5462 seedlings/ha. Although CWD covered only 4% of the forest floor, 43% of all seedlings were growing on this substrate. The density of seedlings growing on dead wood depended on the decay stage of the wood (χ^2 = 2.219; df = 7; p < 0.001). *P. abies* regeneration increased beginning with decay stage 4 (Fig. 1). The highest density of seedlings occurred on well decomposed wood in decay stages 5-7, reaching 1300 individuals per 100 m^2 for wood in decay stage 7. A slight decrease in density was present for the most decayed logs (decay stage 8) (Fig. 1). The same pattern was observed for the number of logs colonized by *P. abies* seedlings. Beginning with decay stage 4, over 60% of logs were colonized (Fig. 2). With advanced decomposition, the number of logs densely colonized

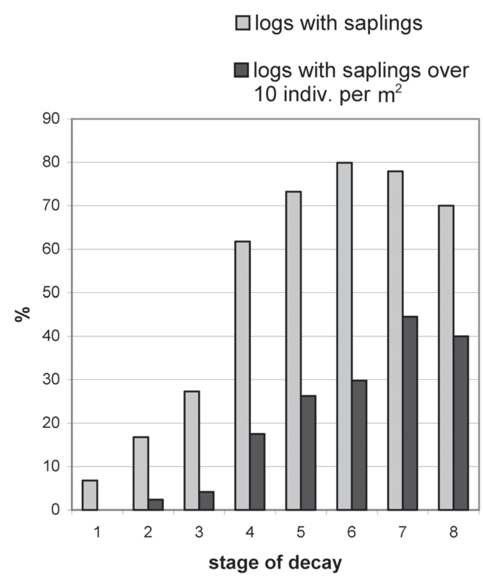

Fig. 2. Percentage of logs in different decay stage colonized with saplings.

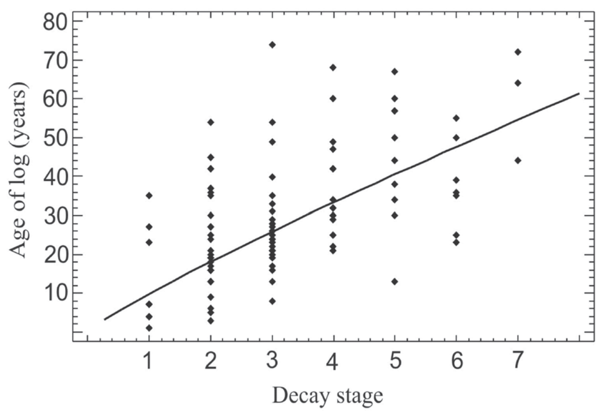

Fig. 3. The relationship between the age of logs (number of years since tree death) and the decay stage. Based on cross-dated samples.

by seedlings (10 or more individuals per 1 m^2) increased, reaching over 40% for the most decomposed logs.

The residence time was estimated using 103 precisely cross-dated logs in decay stages 1-7. It was not possible to cross-date any of the logs in stage 8. Variations in the age of logs within successive decay stages were high but the differentiation of the age of logs among the respective decay stages was statistically significant (ANOVA: $F = 10.1$; df = 5; $p < 0.001$) (Fig. 3). There was no significant correlation between the diameter and the decay rate (the age in decay stages). Weak negative correlation ($r = -0.34$; $p < 0.005$) was observed only in the first two decay stages.

Estimating the age of seedlings using the number of

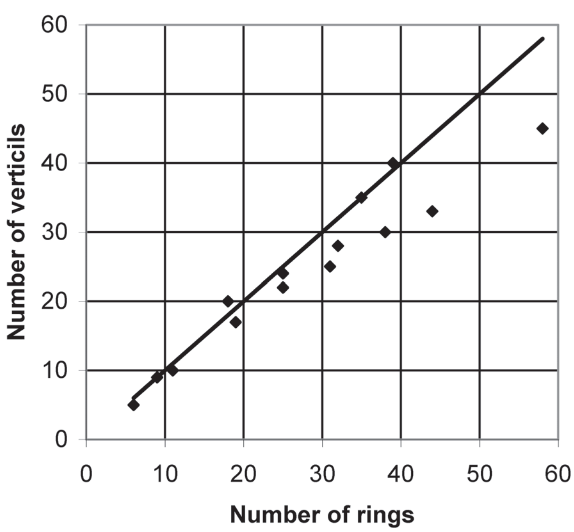

Fig. 4. Relation between the number of verticils at the leader shoot and the number of rings in root collar. Line indicates the same values for both methods of the estimation of seedling age.

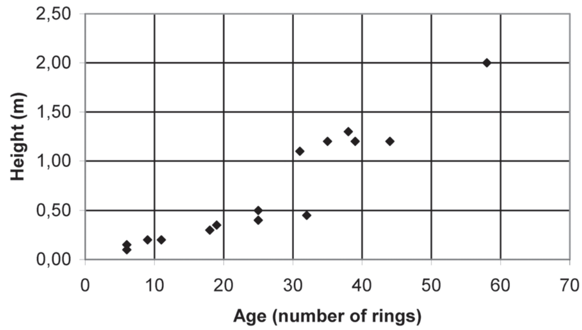

Fig. 5. Seedling height in relation to their age.

verticils was precise ($r = 0.97$; $p < 0.05$) (Fig. 4). For seedlings up to 20 years, the number of verticils and scars visible closely corresponds to the number of tree rings in the root collar. The age of seedlings over 30 years may be underestimated. The difference between the estimated age and the number of rings in the root collar in the case of individuals aged 40-60 years exceeded 10 years in some cases. Over or underestimation of age using this method might be neglected for the purposes of this study when one takes into consideration the problems of precise determination of the age for slow growing *P. abies* based on the number of rings (DesRochers & Gagnon 1997; Niklasson 2002). In addition, *P. abies* grows very slowly on log substrates, achieving heights of 0.5 m after ca. 25 or more years (Fig. 5).

The number of seedlings decreases on logs of all decay stages with an increase of seedlings age (Fig. 6). Among the seedlings growing on wood, almost 80% have germinated over the last 5 years, 15% were aged 6-10 years and 3% were aged 11-15 years. The seedlings older than 16 years constituted only 2% of all recruitment growing on dead wood. Beginning with decay stage 5, the age structure of regeneration changes only slightly with progressive decomposition. The density of the youngest seedlings on wood in decay stages no. 5-7 reached up to 1000 individuals per 100 m^2. A slightly lower density was observed on the most decomposed logs (744/100 m^2). The density of seedlings aged 6-10 years growing on wood in the four most decayed stages numbered around 200 per 100 m^2. The density of seedlings aged 11-15 years on logs in decay stages 5-8 fluctuated between 20 per 100 m^2 (decay stage 8) and 53 per 100 m^2 (decay stage 7). Seedlings older than 45 years appeared on wood in the four most decayed stages with 2-4 individuals per 100 m^2.

The age structure of regeneration is greatly affected by mast years. The abundance of seedlings in the first five year interval was dominated by individuals germinated after the mast year in 1995. The next interval of 6-

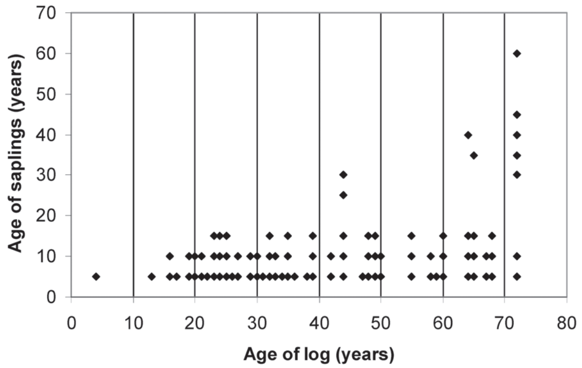

Fig. 7. The age structure of regeneration growing on cross-dated logs.

10 years was made up mostly of seedlings established after the mast year in 1992. Similarly, the age class of 11-15 years consisted mostly of seedlings that survived after the mast year in 1988. However, there was no data relating to the size of the seed crops in these mast years.

Using the age structure of regeneration growing on cross-dated logs enabled observation of the colonization occurring over the past few decades (Fig. 7). The youngest log colonized by seven individuals was only four years old (calculated since tree death). Among the 15 logs cross-dated to 13-19 years, eight were colonized by seedlings. On a log aged 16 years (tree died in 1985), except for the seedlings from the cohort germinated in 1996, five individuals from an older cohort germinated in 1993 were noted. These individuals must have colonized the log eight years after tree death and they must have survived until at least 2001. The youngest log colonized by the third cohort (13 year old seedlings) was cross-dated at 23 years. Among the oldest cross-dated logs, a 64 year old log was colonized by 40 year old seedlings. Four *P. abies* seedlings ca. 60 years old were growing on the oldest cross-dated log (aged 72 years).

Discussion

Although CWD covered only 4% of the forest floor, 43% of all seedlings were growing on it. This resulted in almost a 20 times higher density of spruce regeneration compared with mineral soil. This observation confirms that decaying wood is a very important substrate for the regeneration of *P. abies* (Mayer et al. 1972; Holeksa 2001; Korpel 1989; Zielonka & Piątek 2004; Hytteborn & Packham 1987; Kuuluvainen 1994).

Seedlings seldom appear on relatively fresh logs below decay stage 4. Only a small percentage of such logs was colonized by single saplings. The highest abundance of *P. abies* recruitment was observed on logs

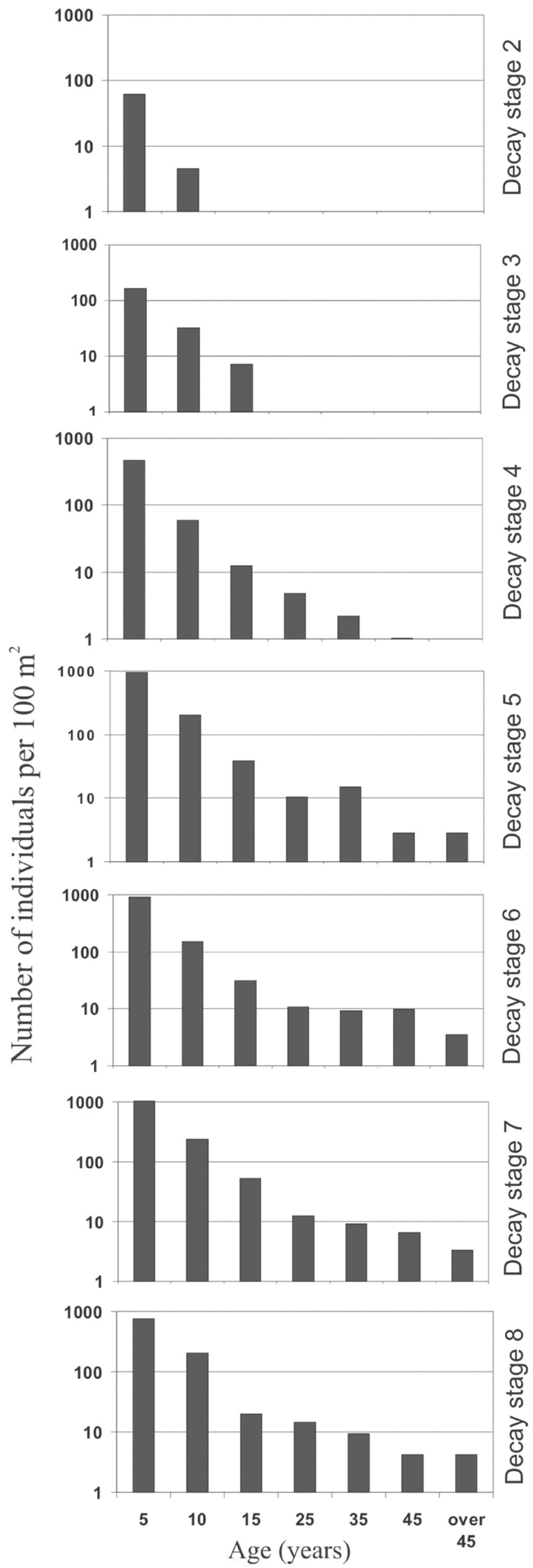

Fig. 6. The age structure of *P. abies* regeneration growing on the different decay stages (logarithmic scale).

in decay stages 5-7. The increase in colonization with increasing decay probably results from physical and chemical changes in the substrate. The cracking of the surface of wood forms crevices that enable the accumulation and holding of seeds. The density of wood decreases and the area to volume ratio grows and the opening of tracheids forms a capillary system that substantially increases the water holding capacity of logs (Käärik 1974; Sollins et al. 1987). Along with the decay process, wood is colonized by microorganisms, fungi and invertebrates, which contribute to an increase in nitrogen (Jurgensen et al. 1987; Hendrickson 1991; Wells & Boddy 1995). Fungus mycelium may transport macro-elements, including nitrogen compounds, from soil to woody debris that directly adheres to the ground (Zimmerman et al. 1995).

Simultaneous colonization of logs with epixilic mosses and liverworts (Hörnberg et al. 1997) and vascular plants (Zielonka & Piątek 2004) may also improve regeneration due to mychorrizal interactions (Miller et al. 1983; Eissenstat & Newman 1990; Nilsson et al. 1993). Also, it is noteworthy that the density of seedlings decreases on the most decayed logs (decay stage 8). Nakamura (1987), Harmon & Franklin (1989) and Holeksa (1998) suggested that this is a result of more intensive competition with other plant colonists, mostly vascular plants and ferns that grow faster and thus overshadow *P. abies* seedlings.

The optimum conditions for germination and further growth of *P. abies* last for ca. 30-60 years after tree death, which corresponds to decay stages 4-7. This time period seems to be necessary to transform a freshly fallen tree into a suitable substrate for *P. abies* regeneration in sub-alpine conditions. However, observation of the age structure of regeneration growing on cross-dated logs (Fig. 7) clearly indicates that the first seedlings may germinate on a log even during the second decade after tree death and survive for following tens of years. Their slow growth is possibly due to the gradual progressive decomposition of wood.

The rapid colonization of decaying wood requires that there be no interval between tree death and tree fall. In sub-alpine forests, there are two main factors responsible for *P. abies* mortality. The most important factors, wind and snow, are responsible for uprootings and stem breakages. In this case, stems become part of the forest floor immediately, which accelerates the decomposition process. The other cause of *P. abies* mortality is by fungal pathogens and bark beetle (*Ips typographus*), which lead to the formation of standing snags. *P. abies* snags may stand up to 20 years before falling (Holeksa 1998; Siitonen 2001; Storaunet & Rolstad 2002), which may considerably inhibit wood decomposition. This may explain the variability in the decay rate, especially in the case of the initial decay stages. However, it was not possible to estimate the lag between death and fall of tree in this study.

Logs, irrespective of their decay stage and age, are dominated by young seedling age classes. As much as 98% of all *P. abies* regeneration on dead wood has germinated over the last 15 years. Dead logs continously provide favourable conditions for the germination of *P. abies* seeds. This results partly from the decay process of dead boles itself: constant formation of crevices and the falling off of outer layers and exposure of new surfaces of rotten wood that may host seedlings (Harmon & Franklin 1989). On the other hand, due to the high mortality of *P. abies* during juvenile growth (Yli-Vakkuri 1963; Leemans 1991), older seedlings are replaced by a new cohort after a subsequent mast year.

P. abies is regarded as a shade tolerant species but unfavourable light conditions might be the limiting factor of growth, at least for older saplings under closed canopies. The presence of gaps and canopy discontinuity is necessary for further successful growth of *P. abies* (Drobyshev 1999; Holeksa & Cybulski 2001; Diaci et al. 2005; Metslaid et al. 2005). The mean volume of living trees (454 m^3/ha in my study plots) was similar to other observations from undisturbed sub-alpine forest in Carpathians (Jaworski & Kaczmarski 1989; Holeksa 2001). Holeksa (2001) measured 407 m^3/ha in one continuous 14 ha plot in Babia Góra Mts. This may indicate that light conditions in study plots were typical for closed canopy stands. This might explain the slow growth of *P. abies* seedlings, where a height of only 1m is achieved after ca. 30 years. The potential of such a recruitment bank present on decaying logs which would appear following intensive post disturbance openings are crucial for the replacement of *P. abies* generations.

Acknowledgements. This study was supported by State Committee for Scientific Research (KBN project no. 2P04F 008 26). The authorities of the Tatra and the Babia Góra National Park are thanked for permission to collect data. I would like to thank Jan Holeksa for valuable discussion on the manuscript and two anonymous reviewers for useful comments and suggestions. I am also grateful to Peter White for helping with language editing.

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Received 9 November 2005;
Accepted 6 July 2006;
Co-ordinating Editor: P.S. White.