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Early Effects after Forest Disturbance in Decomposition of Trees in Two Windthrown Areas in East Estonia

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Abstract

Coarse woody debris (CWD), represented by logs and snags (>10 cm in diameter and >1.3 m in length/height), were sampled from two Eastern Estonian windthrow events (Tudu and Halliku), where storm occurred in the summers of 2001 and 2002. CWD was sampled to identify factors that affect early wood decomposition and changes in wood density. Tree species sampled included Norway spruce (*Picea abies* (L.) Karst.) and birch (*Betula* spp.). In total 944 subsamples were taken from sample trees on permanent sample plots located in totally damaged (TD), partly damaged (PD) and control areas with no damage (ND). Wood densities after the initial period of decomposition were different, depending on tree species, log or snag position (downed, leaning, standing), damage severity (TD area or PD area) and subsample position on sample disks (inner or outer layer of the disk). Most of the CWD was in the second class of decomposition (color of wood had changed and knife enters 1–2 cm into the wood), with mean CWD densities of 0.483 g cm^{-3} to 0.571 g cm^{-3} for spruce and 0.581 g cm^{-3} to 0.778 g cm^{-3} for birch. Annual decomposition rates ranged from 0.78% to 5.57% for spruce and 2.19% to 7.42% for birch. Downed logs had lower density than leaning logs and standing snags. Snags/logs from TD area had a lower density than snags/logs from PD areas, thus they were decomposing faster.

Key words: dead wood, wood density, decay affecting factors, mixed models, windthrow

Introduction

Coarse woody debris (CWD), is an important component of forest ecosystems (Esseen et al. 1992, Samuelsson et al. 1994, Angelstam 1998, Arsenault 1999, Karjalainen and Kuuluvainen 2002), providing forest-dwelling organisms with habitats. It can be a substrate for detrivores, may act as a nursery site for tree regeneration, and can store substantial amounts of nutrients and carbon (Harmon et al. 1986). Several authors (Haila et al. 1993, Samuelsson et al. 1994, Niemelä 1996, Angelstam 1998, Linder and Östlund, 1998, Kuuluvainen et al. 2005) have emphasized the crucial role of CWD for the biodiversity of boreal and hemiboreal forests. Decaying wood is a short-term sink but a long-term source of organic matter and nutrients to the soil, a habitat for a wide array of organisms, and after humification it is an important component of forest soil (Siitonen 2001).

Environment for decomposition changes as a function of disturbance severity. Most past works has been after relatively small disturbances or have focused on dead wood decomposition in closed forests (Krankina and Harmon 1995, Harmon et al. 2000, Shorohova and Shorohov 2001, Yatskov et al. 2003). However disturbances can be with a different severity and produce dead wood in forests to varying degrees. Infrequent catastrophic disturbances can create as much CWD on a single occasion as the total annual background mortality produces between disturbances (Harmon et al. 1986, Siitonen 2001). A stand-replacing disturbance, such as forest fire or windthrow, can transform most of the living stand into CWD (Siitonen 2001), but disturbance can also be defined as a force that kills at least one canopy tree (Runkle 1985). Thus decay dynamics studies both for/between closed forest and open areas are needed. Conditions/factors that control decomposition in these areas, such temperature, moisture, light conditions, organisms involved, can vary significantly and decomposition rates in initially similar habitats/ conditions but with a different severity of damage can be completely different.

To better understand current and future dynamics of the CWD pool, we need to know not only the stores, but also the turnover or decomposition rates of CWD. The patterns and rates of decomposition of CWD are important for several aspects of forest management: Decomposition rates will determine the longevity and turnover of carbon stored in CWD. This study examines the dynamics of CWD decomposition in permanent sample plots, exploring the environmental conditions and factors influencing the changes in wood density of the two major tree species in the windthrow area of east Estonia (initially similar areas damaged to a varying extent). We defined decomposition as a change in wood density. It was hypothesized: (1) CWD under a partial overstory (partly damaged) decomposes faster due to a more favourable microclimate, (2) because of wood characteristics birch should decompose faster than spruce and (3) log contact with soil is expected to increase decay rates. We also compare our results with those of other studies.

Materials and methods

Study areas

Sites were selected in the Tudu Forest District (59º11' N 26º52' E) and in Halliku Forest District (58º43' N 26º55' E) (Eastern Estonia) in hemiboreal vegetation zone (Ahti et al. 1968), which experienced severe windthrow on 16 July 2001 and 5 July 2002, respectively. The average temperature in the area all over the year is +5.2ºC. The coldest month is February, at –5.7ºC and the warmest is July at +16.4ºC. The average precipitation is 550–650 mm. Norway spruce (*Picea abies* (L.) Karst.) is the dominant species at both sites, with lesser amounts of European aspen (*Populus tremula* L.), black alder (*Alnus glutinosa* (L.) J. Gaertn.), Silver birch (*Betula pendula* Roth.) and downy birch (*Betula pubescens* Ehrh.) (Table 1). The study areas include stands on Eutric Gleysols and Calcaric Cambisols (FAO, ISSS, ISRIC 1998, Reintam et al. 2001), *Filipendula* and *Myrtillus* forest site types (Lõhmus 1984) being most commonly represented (Ilisson et al. 2005). The detailed description of how the sample plots were established and how the CWD volume after windthrow was measured, has been published in Ilisson et al. (2005).

No salvage logging occurred between windfall and measurements. Fieldwork occurred in the early summers of 2003, 2004 and 2005 (measurements started and plot system marked after disturbance). Formerly the forests were under protection (landscape protection area) where there has been no management intervention in decades. The stand ages in the study area were in range from 110 to 160 years (Table 1). In study area Ilisson et al. (2005) found that European aspen (*Populus tremula* L.) was the species most prone to uprooting, while black alder (*Alnus glutinosa* (L.) J. Gaertn) was most likely to have stem breakage. The proportion of uprooting and stem breakage was relatively similar among the Norway spruce and birch.

Table 1. Description of the study plots after windstorm in Tudu and Halliku study area: "Volume" describes the volume of downed wood for completely destroyed plots, volume of standing trees for control plots and volume of downed wood/ volume of standing trees for partially damaged area. Sp – Norway spruce (*Picea abies* (L.) Karst.), As – European aspen (*Populus tremula* L.), Bi – birch (*Betula pendula* Roth.), Al – black alder (*Alnus glutinosa* (L.) J. Gaertn), Ac – common alder (Alnus incana (L.) Moench); Ah – ash (*Fraxinus excelsior* L.) (adapted from Ilisson et al. 2005)

Location	Damage type	Site type	Composition (percentage from stem numbers)	Year of Orgin	Volume (m^3/ha)
Tudu	Totally	*Myrtillus*	45Sp 43As 12Bi	1865	616
Tudu	Control	*Myrtillus*	73Sp 11As 7Al 5As 5Bi	1875	376
Tudu	Control	*Myrtillus*	44Sp 28Bi 15As 12Al	1875	367
Tudu	Totally	*Filipendula*	76Sp 12Bi 6Al 5As	1865	397
Tudu	Harvested	*Myrtillus*	46Bi 27Sp 19As 7Ac	–	
Tudu	Partly	*Myrtillus*	57Sp 27As 13Bi 3Al	1845	238/271
Tudu	Control	*Myrtillus*	47Sp 29Bi 18As 7Al	1875	342
Tudu	Totally	*Myrtillus*	72As 26Sp 2Bi +Al	1845	651
Tudu	Harvested	*Filipendula*	62Bi 38Sp	–	
Halliku	Harvested	*Myrtillus*	44As 37Bi 11Al 5As 3Sp	–	
Halliku	Harvested	*Myrtillus*	40Bi 30Sp 29As 1Ma	–	
Halliku	Partly	*Filipendula*	53Sp 30Al 13Bi 2Ac 2As	1873	138/217
Halliku	Control	*Filipendula*	57Al 28As 9Ac 3Bi 3Sp 1Ma	1958	292
Halliku	Partly	*Myrtillus*	76Sp 16As 6Bi 1As 1Ac	1893	225/105
Halliku	Partly	*Filipendula*	82Al 11Sp 6As	1898	277/264
Halliku	Totally	*Myrtillus*	82Sp 17Bi 1As	1893	231

Randomly selected sample trees originated from three variants of damage severity: (i) totally damaged areas (TD) with total canopy destruction (all trees damaged by storm), (ii) partly damaged areas (PD) with partial canopy destruction (approximately half of the trees damaged and distributed uniformly), (iii) control areas (ND) with no damage (living trees), taken as close as possible to TD and PD areas. In total we analysed 334 sample logs and snags (153 logs/snags from TD area, 160 logs/snags from PD area and 21 living trees from ND area). The sample snags (standing dead) or logs (dead downed or leaning) were randomly selected from spruce (*Picea abies* (L.) Karst) and birch (*Betula* spp.).

Field and laboratory measurements

Sampled living trees and CWD in the form of logs and snags (>10 cm in diameter and >1.3 m in length/ height) were categorized into five decay classes based on visual characteristics linked to the degree of decomposition and the knife-based system described in Renvall (1995) and Tukia et al. (2001). Log length, base and top diameters and diameter at breast height were measured. Sample disks (2–5 cm thick) were taken from three cross sections, located along the height/length of each log or snag examined. The first cross section was taken at the height/length of 1.3 m from the root collar/thick end of the trunk. The second disk was taken from the middle of the log/snag. And the third cross section was taken from close to the top (the diameter of the third disks should be at least 10 cm to get four wood subsamples from each disk (Figure 1). If the sample log was broken and shorter than 6 m, only two cross sections were taken: at 1.3 m and close to the top, but with disk diameter not less than 10 cm. The outermost diameter, longitudinal and radial thickness of bark were measured at two points on each disk (where the values were highest and lowest, as assessed visually). Bark (not analysed in this study) was removed from wood and the wet mass of each sample was determined (with precision 1 g). Wood subsamples (ca 20 g) were taken from each disk, weighted and air-dried in paper bags to stop decomposition. The subsamples were taken from different locations on the disk depending on its diameter, as shown in Figure 1, to find out how different parts of the tree are decomposing. The data set for analyses included a total of 944 subsamples from 174 spruces and 160 birches.

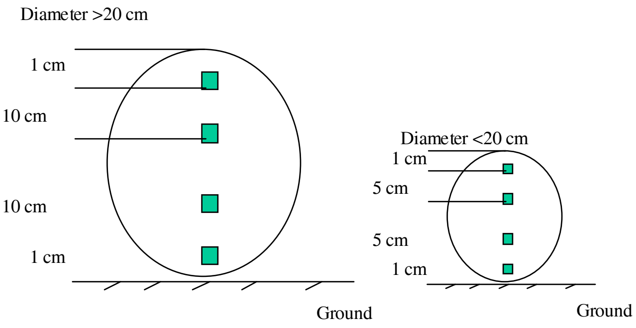

Figure 1. The location of subsamples depended on disk diameter. On disks with diameter >20 (diameter without bark) the subsamples were taken at 1 cm from the edge of the disk and at 10 cm from the edge of the disk. On disks with diameter <20 (minimum 12 cm), the subsamples were taken at 1 cm and at 5 cm from the edge of the disk

Dry mass of subsamples was measured after oven drying at 65 ºC to a constant mass (precision 0.01 g). Sample volume was determined by water displacement technique (xylometer) following the procedures of Ilic et al. (2000). Wood samples were saturated before volume measurements, to avoid water absorption. As the density of water under laboratory conditions is $1\ \mathrm{g\ cm^{-3}}$, the weight of the displaced water equals the volume of the sample. The basic density (d, in $\mathrm{g\ cm^{-3}}$) of each sample was calculated by the formula

$$d = m_0/V \qquad (1)$$

where m_0 is the dry mass of the sample and V is the volume of the fully swollen sample.

Wood decomposition is a fairly well-understood process, in which the dry density (or mass) loss per time unit is roughly proportional to the amount of woody material remaining. This process can be described by the negative exponential model (Olson 1963, Harmon et al. 1986):

$$X=X_0\, e^{-kt} \qquad (2)$$

where X_0 is the initial dry wood density, X is the dry density after t years, and k is the decomposition rate constant.

Decomposition rate is generally expressed through a constant k (percent mass loss $\mathrm{year^{-1}}$) and is best determined for long-term studies (Harmon et al. 1986, Mackensen et al. 2003).

Statistical analysis

Prior to the statistical analysis, we transformed wood density values with the binary logarithm ($\log_2 n$) to approximate residual distribution of the variable to the normal distribution assumed in statistical procedures. On account of multiple observations per log (subsamples within disk within log) the main analysis were carried out with SAS procedure 'Mixed' (Release 8.2). This procedure realises general linear mixed variance analysis (SAS Institute Inc. 1999), which in the present case helps one to test whether, and how, the tree species, damage severity, time elapsed from damage, damaged tree position and the subsample position in the disk determine the CWD density. The results of the analysis are presented in a combined ANOVA table (Table 3).

A problem arose when we tried to separate the partial effect of each factor from the summary effect of all factors. To overcome this problem, we have used two types of mixed analyses. In Type 1 ANOVA (SAS Institute Inc. 1999), researcher arranges factors according to the priority they assign them (arranged according to the earlier literature and study results). The first factor is considered to have the highest priority and if it happens to be correlated with the tree density, this correlation is interpreted as the effect of this factor only even if it is actually caused by other factors. The second and the following factors in the ordering are treated in a similar way, assigning the remaining influence to factors in accordance with their position in the ordering.

Type 3 Analysis attempts to assign to each factor the effect that cannot be related with other factors. If the effect of a factor appears to be significant, the P-value expressing this significance is considered as responsible for the given factor only. Otherwise, if the effect can be related also with other factors, it may not be declared as proved even if it really influences the wood density. This estimation policy is partially described also in the caption of Table 3.

Results

The mean wood density of spruce and birch differed after three years of the decomposition (Table 3, Row 2), and was higher for the birch (Table 2). From other factors, the damage severity had a clear correlation with the CWD wood density (Table 3, Row 4). Table 2 showed that in more damaged areas the density of wood was lower than in less damaged areas for both tree species.

The mean CWD density decrease compared with undisturbed forest trees was observed 2–3 years after disturbance. The wood density of living trees from control areas was on average 0.571 g cm^{-3} for spruce and 0.778 g cm^{-3} for birch. These values we have taken also as 0-level (wood density before disturbance). Two, or three years after disturbance the downed spruce logs had, on average, a density of 0.483 g cm^{-3} in Tudu and 0.493 g cm^{-3} in Halliku (Table 2). In areas with different damage severity the densities of decaying spruce logs/snags ranging from 0.483 g cm^{-3} to 0.567 g cm^{-3} (Table 2). For birch the density changes were even larger, ranged from 0.581 g cm^{-3} to 0.739 g cm^{-3} (Table 2). Three years after disturbance the downed birch logs had average density 0.626 g cm^{-3} in Tudu and 0.581 g cm^{-3} in Halliku (Table 2). At that time, 13% of spruce trunks were in the in first decay class, 79% in the second decay class, and 8% in the third decay class. In the case of birch, 18% from selected trunks were in the first decay class, 73% in the second decay class, and 9% in third decay class.

Table 3. Analysis of logarithmic CWD density: results of I and III type ANOVA tests. Factors (F) – fixed, (R) – random. Species – Spruce or Birch, Region – Tudu or Halliku windthrow. Damage – damage severity of study area (not damaged, partially damaged, totally damaged), Snag/Log position –downed, leaning or standing, Disk position – position of the sample disk on the trunk (three positions for a tree), Core position – position of the subsample on the sample disk (see Figure 1), D – sample disk diameter, DF – numerator and denominator degrees of freedom for the F-test. For F-factors the P-value corresponds to the null hypothesis 'Factor has no effect on CWD density' (n.s. – not significant), for R-factors the hypothesis is 'Factor has not caused additional variability of CWD density'. Column 'Nested/Grouped within' lists numbers of factors that might have modified the effect of a fixed row factor, or the factors for which levels the residual variance of dependent variable may differ. σ^2_ε and ρ are parameters of the covariance structure AR(1) characterizing dependence between the four subsamples on the sample disk (Figure 1): σ^2_ε is the residual variance of LDensity and ρ is the correlation between the adjacent subsamples on the sample disk. 'Major factors in Type I' are fixed factors, influence of which is eliminated before the estimation of the row factor effect. Denominator DF = 188 corresponds to the Model used for calculating Table 2.

No	Factor	Factor (type)	Nested/	DF	ANOVA	Major	P-value
1	0	Tree (R)	1	–	σ^2_ε=0.013	–	< 0.0001
2	1	Species (F)	–	1/188	I, III	–	< 0.0001
3	2	Region (F)	–	1/188	I, III	1	n.s.
4	3	Damage (F)	–	2/188	I, III	1, 2	<0.0001
5	4	Snag/Log position (F)	–	2/188	I	1	<0.0001
6	4	Snag/Log position (F)	–	2/188	III	–	n.s.
7	5	Core position on disk	1, 4	14/188	I, III	1, 2, 4	n.s.
8	6	Core position: birch	0, 1	–	AR(1)	–	n.s.
9	6	Core position: spruce	0, 1	–	AR(1),	–	0.0044
10	7	Time (F)	1, 4	6/188	I, III	1, 2, 4	n.s.
11	7	Time (F)	1, 4	6/188	I	1	<0.0001
12	8	Disk position (R)	0	–	–	–	0.0104
13	9	Disk diameter (F)	–	1/188	I, III	1–4, 6, 7	0.0312

Table 2. The average densities of wood samples from areas with a different severity of damage, where TD is a totally damaged area, PD is a partly damaged area and ND is a control area with no damage (living trees)

		Halliku					Tudu		
Area	Species	Snag position	n	Average density g cm^{-3} (SE)	Area	Species	Snag position	n	Average density g cm^{-3} (SE)
TD	Spruce	Downed	16	0.493 (0.013)	TD	Spruce	Downed	16	0.483 (0.014)
		Leaning	14	0.528 (0.023)			Leaning	16	0.527 (0.008)
		Standing	10	0.532 (0.017)			Standing	8	0.567 (0.040)
PD	Spruce	Downed	16	0.495 (0.016)	PD	Spruce	Downed	16	0.537 (0.022)
		Leaning	16	0.520 (0.014)			Leaning	16	0.547 (0.014)
		Standing	10	0.550 (0.019)			Standing	8	0.559 (0.021)
ND	Spruce	Control	12	0.571 (0.026)	ND	Spruce	Control	12	0.571 (0.025)
TD	Birch	Downed	12	0.581 (0.024)	TD	Birch	Downed	16	0.626 (0.014)
		Leaning	15	0.641 (0.020)			Leaning	8	0.632 (0.014)
		Standing	10	0.661 (0.030)			Standing	12	0.634 (0.027)
PD	Birch	Downed	8	0.669 (0.032)	TD	Birch	Downed	14	0.659 (0.033)
		Leaning	16	0.645 (0.016)			Leaning	16	0.673 (0.018)
		Standing	12	0.693 (0.022)			Standing	12	0.739 (0.031)
ND	Birch	Control	9	0.778 (0.029)	ND	Birch	Control	9	0.778 (0.029)

Decomposition rate constants, based on percentage of density remaining, ranged from 0.0078 year^{-1} to 0.0557 year^{-1} for spruce and from 0.0219 to 0.0742 year^{-1} for birch (Table 4). The results of our study revealed that the wood decay (wood density changes) also dependent on log or snag position (Table 3 Row 5). Figure 2 and table 4 indicated that downed logs were decomposing faster than leaning logs and standing snags. This was a simple expectation but Row 6 of Table 3 shows that the imbalance of dataset may explain this dependence also with the impact of other factors apart from snag/log position. In case of spruce, downed logs were decaying faster (losing density) in all areas regardless of damage severity (Figure 2). The average decay rate constant for lying spruce logs in a totally damaged area was 0.0557 year^{-1}, but for standing snag in a partly damaged area the decay rate constant was 0.0078 year^{-1} (Table 4). The average decay rate (all samples together) for spruce in completely damaged area was 0.0305 year^{-1} and in partly damaged area 0.0189 year^{-1} The same tendency was observed in the case of birch, where downed logs were losing their density faster than leaning and standing logs/snags (Figure 2). The average decay rate constant for lying birch logs in a totally damaged area was 0.0742 year^{-1} and for standing snags in a partly damaged area 0.0219 year^{-1} (Table 4). The average decay rate constant for birch in a totally damaged area was 0.0724 and in a partly damaged area 0.0452 year^{-1}.

Table 4. Estimated decomposition rate constants (k) for spruce and birch

Species	Damage severity	Snag/Log position	n	X_0	k (year)	R^2
Spruce	Totally damaged	Lying	43	0.5597	-0.0557	0.2365
		Leaning	41	0.5602	-0.0249	0.053
		Standing	29	0.5598	-0.0109	0.0084
	Partly damaged	Lying	43	0.55	-0.0255	0.0407
		Leaning	41	0.5561	-0.0233	0.0233
		Standing	29	0.5631	-0.0078	0.0064
Birch	Totally damaged	Lying	36	0.739	-0.0742	0.2835
		Leaning	29	0.7604	-0.0722	0.3384
		Standing	30	0.7687	-0.0708	0.3161
	Partly damaged	Lying	30	0.7687	-0.0641	0.1854
		Leaning	40	0.7494	-0.0496	0.2144
		Standing	32	0.57	-0.0219	0.0453

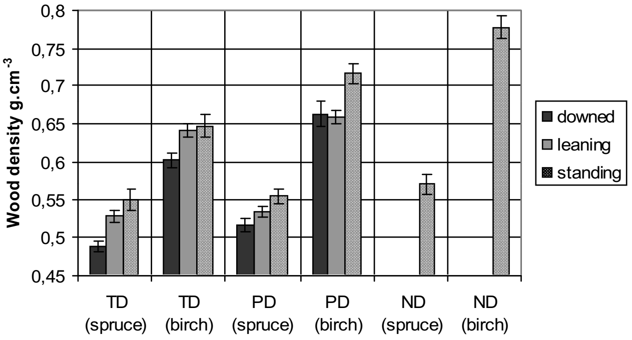

Figure 2. The wood density in downed, leaning and standing spruce and birch logs/snags on totally and partly damaged areas compared with living tree density. Where TD means totally damaged area, PD means partly damaged area and ND means control area with no damage. Error bars show standard

Several rows (Rows 7, 8, 9) in Table 3 present the effects of subsample position on the disk taken from tree trunk. Two random factors describe this position; these are the sample disk position on the log and the subsample position on the sample disk. The sample disk position factor had only marginal confidence (Table 3, Row 12, P = 0.0104). Having in mind that Table 3 presents results of a multiple testing, this P-value did not reject the null hypothesis and, therefore, the effect of disk position was not proved. The other factor was the subsample position on the sample disk (Figure 1). This factor was presented by a fixed factor and by a random factor. When the random factor was taken into account, the effect of the fixed factor was not significant (Table 3, Row 7). At the same time the random factor was significant for spruce (Table 3, Row 9). The structure of the covariance applied AR(1) had a significant negative correlation parameter ρ (ρ = –0.37, P = 0.0044, Table 3, Row 9). The minus sign means that when moving from the upper edge of the spruce subsample disk to the lower edge, density changes could be observed and lower edge (close to the ground) has lower wood density.

Discussion and conclusions

The results of our study revealed, that 2–3 years after disturbance most of the trees were in the second decay class (more than 70% for both spruce and birch). Harmon et al. (2000) and Shorohova and Shorohov (2001) found similar results for the same forest zone in north-western Russia (St. Petersburg and Novgorod region located at about 59° N and between 31 and 32° E). According to Shorohova and Shorohov (2001), birch logs/snags that are in the first decay class have been decaying on average 1.6 years and log/snags that are in the second decay class have been decaying on average 3.3 years. Spruce logs that are in the first decay class have been decaying on average 3.1 years and logs/snags that are in the second decay class have been decaying on average 6.5 years.

Decomposition rates and density changes for different tree species are different (Harmon et al. 1986, Boddy 2001, Krankina et al. 2002, Yatskov et al. 2003). Wood density of living trees within tree species varies as well. In the boreal zone, deciduous trees generally decompose faster than coniferous trees, because the gymnosperm wood is less complex and contains less living tissue than that of angiosperms (Harmon et al. 1986). Birch also retains its bark through the entire decomposition process (Krankina et al. 1999), which prevents the sapwood and the heartwood from sloughing and decay processes can be quite rapid (Yatskov et al. 2003) and take place in the inner and the external layers. Moreover, wood of coniferous snags/logs is often impregnated with resin, which prevents decay (Tarasov and Birdsey 2001). Different studies confirmed that log/snag position (contact with soil) is an important factor influencing wood decomposition (Hytteborn and Packham 1987, Næsset 1999, Shorohova and Shorohov 2001, Mackensen and Bauhus 1999), as those cross sections that had direct contact with the forest floor were decomposing faster than those held in the air. Differences in decomposition rates of logs and snags indicated also, that disturbances creating snags increase overall turnover time of CWD. In the totally damaged area, trees killed in the storms are the main source of CWD in the stand for at least several decades. Total CWD volume within the stand starts to decline after the disturbance. As the stands develop (during succession), CWD volume produced by annual mortality increases, first mainly due to competition and self-thinning, and later because of exogenous disturbances (Siitonen 2001). In partly damaged areas CWD total volume is not declining after disturbance, it will increase during some years after disturbance because some trees, that survived the initial disturbance, are weakened by damage and will die later (finally death is caused by other factors, such as insects, fungi etc.).

In our case, at the beginning of the decomposition processes, downed logs were decaying faster than leaning logs and remarkably faster than standing snags. Felling makes wood available for colonization under conditions that are relatively non-stressful (Boddy 2001). Primary colonizers (microbes, fungi) can become established from exposed log ends, wounds and via propagules latently present within the wood before felling. Also contact with soil increases moisture levels inside the log. Hytteborn and Packham (1987) and Nęsset (1999) found that the decay rate (density loss) for spruce log is most rapid when the logs are in direct contact with a moist forest soil. Næsset (1999) also found that in case of spruce the plots subjected to limited solar exposure showed the most rapid decomposition (logs will decompose faster in closed forest stands than in open areas). From our study it appeared that at least at the beginning of the decay processes TD areas (open areas) were decaying faster than PD areas (stands with closed canopy). The reason may be that after disturbance in TD area the transpiration capacity of trees is low or is absent and the areas will become wet but in the same time temperature is increasing as the area is open to the sun light. So as the moisture level stays high, the wood material is not drying/seasoning through and in these warm and moist conditions is preferential for colonization of the wood material by decay affecting organisms (fungi). Unfortunately the species composition of fungi and their influence on wood decomposition was not studied in this study. In PD areas, at least half of the stand remains in place and the transpiration continues. Formally though, an alternative explanation exists that trees having a lower wood density have larger probability of being severely damaged by wind, which means that trees in TD areas may have lower wood density and they are decaying faster. Ilisson et al. (2005) found, that in the same study area, the probability of uprooting increased with increasing diameter of Norway spruce and birch, but on average the proportion of uprooting and stem breakage was relatively even. In our study we also tested the effect of time. As the amount of wood decay was dependent on tree species and on log/snag position, we tested the linear effect of time (2 or 3 years) elapsed from the damage. But time did not become clearly significant. Annual decomposition rates varied among the species and also among snags or logs. The average decay constant for spruce, expressed through decomposition constant k, was 0.025 year^{-1} and for birch 0.059 year^{-1}. For comparison of our data with other studies we need to compare our data with the results observed in similar boreal forests. Krankina and Harmon (1995) found that the average decay constant for spruce in north-western Russia was 0.034 year^{-1}. Similar result was found by Næsset (1999) in Norway, where decay constant was 0.033 year^{-1}. Analogous results were found byYatskov et al. (2003) and Tarasov and Birdsey (2001). Our lower decay constant can be explained with extrapolation, because data are available for 3 years. But as Harmon et al. (2000) and Yatskov et al. (2003) have found, that spruce decay process is going through three phases (slow, rapid, and moderately slow), we can predict that spruce snags/logs in or case are in slow phase of decay. In case of birch, Harmon and Krankina (1995) found that average decay constant was 0.045 year^{-1}. Yatskov et al. (2003) found, that decay constant for birch snags was 0.027 and for birch logs 0.054 year^{-1}.

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БЫСТРЫЕ ИЗМЕНЕНИЯ В РАЗЛОЖЕНИИ ДЕРЕВЬЕВ ПОСЛЕ ПОВРЕЖДЕНИЯ ДРЕВОСТОЕВ НА ДВУХ УЧАСТКАХ ВЕТРОВАЛА В ВОСТОЧНОЙ ЧАСТИ ЭСТОНИИ

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Резюме

Крупные обломки древесины (КОД), представленные бревнами и сучьями (>10 см в диаметре и >1,3 м в длину/высоту) были собраны на двух участках после ветровала в восточной части Эстонии (Туду и Халлику). КОД были собраны для того, чтобы установить факторы, влияющие на разложение ранней древесины, и изменения в плотности древесины. Исследовались древесные обломки ели (*Picea abies* (L.) Karst.) и березы (*Betula* spp.). Всего было взято 944 подвыборки древесины у модельных деревьев на постоянных опытных участках, которые расположены на полностью поврежденных (ПП), частично поврежденных (ЧП) и на контрольных, без повреждений (БП), территориях. Начальные плотности древесины различались в зависимости от породы дерева, от положения бревна или сука (лежащий, находящийся под наклоном, стоящий), от серьезности повреждения (ПП участок или ЧП участок), и от расположения подвыборки на пробном диске (внутренний или внешний слои диска). Большая часть КОД была отнесена ко второму классу разложения древесины (цвет древесины изменился и нож входил на 1–2 см в древесину) со средней плотностью КОД от 0,483 г см$^{-3}$ до 0,571 г см$^{-3}$ для ели и от 0,581 г см$^{-3}$ до 0,778 г см$^{-3}$ для березы. Лежащие бревна имели меньшую плотность, чем находящиеся под наклоном бревна и стоячие сучья. Бревна/сучья, находящиеся на ПП участке имели меньшую плотность древесины, чем бревна/сучья на ЧП участке, и соответственно их разложение происходило быстрее.

Ключевые слова: мертвая древесина, плотность древесины, факторы разложения древесины, смешанные модели, ветровал