Eesti Maaülikool
Estonian University of Life Sciences

DYNAMICS OF LIVING AND DEAD WOODY BIOMASS IN FOREST ECOSYSTEM AFTER WINDTHROW

ELUSA JA SURNUD PUIDU BIOMASSI DÜNAAMIKA TORMIJÄRGSES METSA ÖKOSÜSTEEMIS

KAJAR KÖSTER

A Thesis
for applying for the degree of Doctor of Philosophy in Forestry

Väitekiri
Filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Tartu 2009

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in text by their Roman numerals.

I **Köster, K.,** Jõgiste, K., Tukia, H., Niklasson, M., Möls, T. 2005. Variation and ecological characteristics of coarse woody debris in Lahemaa and Karula National Parks, Estonia. Scandinavian Journal of Forest Research 20(6), 102-111.

II **Köster, K.,** Voolma, K., Jõgiste, K., Metslaid, M., Laarmann, D. 2009. Assessment of tree mortality after windthrow using photo-derived data. Annales Botanici Fennici 46, xx-xx (Accepted).

III **Köster, K.,** Ilisson, T., Tukia, H., Jõgiste, K., Möls, T. 2009. Rapid effects after forest disturbance in decomposition of trees in two windthrown areas in east Estonia. Baltic Forestry X, xx-xx (Accepted manuscript).

IV Ilisson, T., **Köster, K.,** Vodde, F., Jõgiste, K., 2007. Regeneration development 4-5 years after a storm in Norway spruce dominated forests, Estonia. Forest Ecology and Management 250, 17-24.

V **Köster, K.,** Ilisson, T., Jõgiste, K. 2007. Nutrients in coarse woody debris and forest regeneration in windthrow areas. Miškininkystė, Supplement No. 1, 61(1), 13-18.

The contributions of the authors to the papers were as follows:					
	I	II	III	IV	V
Original idea	KK	KJ, KK	KJ, KK	KJ, TI	KK
Study design	HT	KJ, KK	KJ, KK, TI	KJ, KK, TI	KJ, KK, TI
Data collection	KK	KK	KK	KK, TI	KK, TI
Data analysis	KK, TM	KK	KK, TM	TI	KK, TI
Manuscript preparation	HT, KJ, KK, MN, TM	DL, KJ, KK, KV, MM	HT, KJ, KK,	FV, KJ, KK, TI,	KK, KJ, TI
DL – Diana Laarmann; FV – Floor Vodde; HT – Harri Tukia; KJ – Kalev Jõgiste; KK – Kajar Köster; KV – Kaljo Voolma; MM – Marek Metslaid; MN – Mats Niklasson; TI – Triin Ilisson; TM – Tõnu Möls					

ABBREVIATIONS

CWD	coarse woody debris
TD	totally damaged areas with total canopy destruction
PD	partly damaged areas with partial canopy destruction
ND	control areas with no damage (living trees)
LG	logged areas (harvested, material removed)
d	Wood density, g cm^{-3}
m_0	dry mass of wood sample, g
V	Volume of the sample, cm^{-3}

1. INTRODUCTION

Knowledge of forest disturbances and successional processes, including population dynamics of forest-dwelling species is crucial for developing ecologically suitable forest management strategies (Kuuluvainen, 2002) Disturbances exert strong control over the species composition and structure of forests (Frelich, 2002). Among different natural disturbance factors wind damage is playing an active role in the successional cycle of forests (Bouget and Duelli, 2004).

The consequences of wind disturbance can be quite varied, depending on disturbance severity, on forest structure and composition and other characteristics of a specific storm (Lindemann and Baker, 2001). Relatively small disturbances may result in small changes in stand composition, while extensive mortality induced by catastrophic natural disturbances (fires, windthrows, massive insect outbreaks, *etc*.) is followed by the establishment of pioneer plant communities – both tree regeneration and ground vegetation (Gromtsev, 2002). Disturbance can have short- and long term effects, on the secondary succession of vegetation, canopy closure, and dead wood decay (Bouget and Duelli, 2004).

In most disturbance events only a certain proportion of the trees die, this leads to the development of a multilayered, uneven-aged forests (Kuuluvainen, 2002; Rouvinen *et al*., 2002b). In addition to disturbance type and severity, tree succession is influenced by different factors such as the presence and location of seed trees, variability of mast years and species composition of the predisturbance forest. The creation of pits and mounds is also important for tree regeneration and maintenance of tree species mixtures in forests (Hofgaard, 1993; Kuuluvainen, 2002). Several studies have also found that the formation of gaps, through the death of single or groups of trees, is essential for the regeneration processes (Lundqvist and Nilson, 2007).

When a disturbance event kills trees and facilitates and initiates regeneration, it also starts another successional sequence, the decomposition succession of dead trees (Kuuluvainen, 2002). Dead wood, also known as coarse woody debris (CWD), is recognised as an important component of boreal and hemiboreal forest ecosystems linked to biodiversity and ecosystem processes (Samuelsson *et al*., 1994; Angelstam, 1996; Karjalainen and

Kuuluvainen, 2002). When a tree dies, it has only fulfilled a part of its ecological role (Siitonen, 2001). Decaying wood is a short-term sink but a long-term source of organic matter and nutrients (Harmon *et al.*, 1986; Siitonen, 2001), a habitat for a wide array of organisms, a seed bed for trees (Harmon *et al.*, 1986; Kuuluvainen, 2002) and after humification it is an important component of the forest soil (Siitonen, 2001). Standing dead trees (snags), stumps, and fallen logs in different stages of decomposition provide a variety of habitats for decomposers, plants, and animals (Kuuluvainen, 2002).

In natural forests, all dead wood created by disturbances decomposes on sites. In managed forests, the amount of wood left decaying on sites depends on the cutting and utilization regimes (Sippola *et al.*, 1998), but the amount of wood, especially large pieces, will be less than in natural forest (Laiho and Prescott, 2004). Wood of large diameter classes (>20 cm) is particularly important for threatened and rare saproxylic species (Andersson and Hytteborn, 1991; Siitonen, 2001; Rouvinen *et al.*, 2002). One reason for this may be that large trunks decay slower than twigs, branches and small trunks (Harmon *et al.*, 1986). By holding more moisture, they provide continuous and more stable substrate suitable for specialist species.

Stand structure, the arrangement and relationships of live and dead trees, is one of the key attributes of forest ecosystems (Sturtevant *et al.*, 1997; Brassard and Chen, 2006). To understand how disturbances exert different influences over the forest, it is necessary to know the basic concepts and mechanisms of disturbance dynamics and post-disturbance development. Insight into the dynamics of disturbances and into the dynamics of CWD will help land managers understand the impact of disturbances and current management regimes on the CWD cycle, and incorporate this important resource into future plans for more productive, diverse, and healthy forest ecosystems.

2. REVIEW OF LITERATURE

2.1. CWD formation

It is generally acknowledged that natural disturbance is so common that it usually prevents forests from reaching a stable stage (Kuuluvainen, 1994). Disturbance in forest ecosystem varies spatially and temporally from large-scale catastrophic disturbances operating in landscape level to small-scale perturbations operating at the scale of individual tree (Kuuluvainen, 1994). Inputs of CWD come from both the pre-disturbance and current stand and the inputs from each to the total CWD pool varies with the age of the stand (Siitonen et al., 2000; Brassard and Chen, 2008).

CWD is commonly treated as two fractions in studies: standing dead trees and down woody material (Bobiec, 2002; Gromtsev, 2002). In natural forest the CWD dynamics is largely a reflection of time since the last stand-replacing disturbance (Laiho and Prescott, 2004; Brassard and Chen, 2006) and the accumulation of CWD over time will follow a U-shape distribution (Sturtevant *et al.*, 1997; Brassard and Chen, 2006) (Figure 1), where large, post-disturbance inputs of CWD decrease logarithmically while pre-disturbance inputs of CWD increase exponentially, before decreasing slightly. This translates to the high amount of CWD in young, early-successional forests and old, late-successional forests and low levels in mature forests (Brassard and Chen, 2006). The availability of CWD within early stages of forest development is almost entirely dependent on individual stand history – predisturbance debris, disturbance-generated debris, and residual standing trees (Sturtevant *et al.*, 1997). In contrast, CWD within accumulation stage (Figure 1) must be generated by the present stand and is therefore dependent on the standing forest structure (Sturtevant *et al.*, 1997). CWD levels tend to be high following the initial stand disturbance. Residual CWD then declines over time, with little additional input from the regenerating stand. As the stand matures, tree mortality due to competition and small-scale disturbances (gap disturbance) contributes to the CWD reservoir. A gap disturbance is usually a relatively discrete event in time that locally changes tree population structure, resources, substrate availability or the physical environment (Kuuluvainen, 1994).

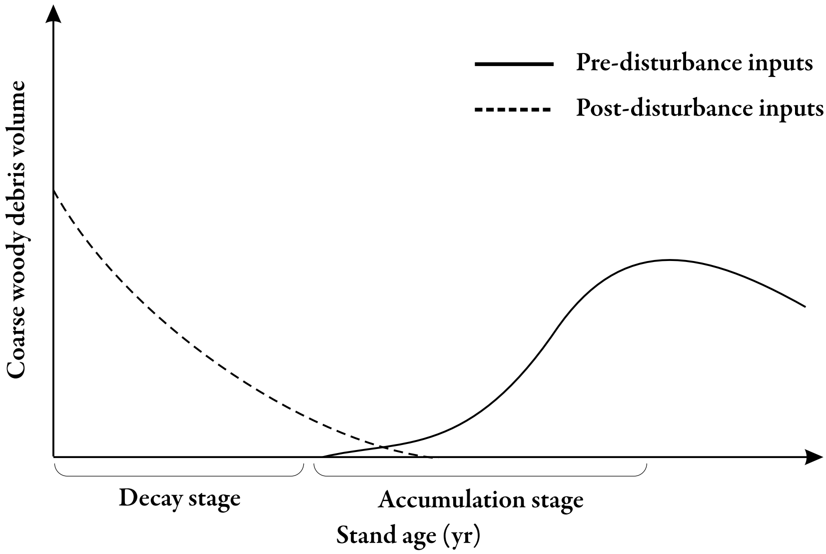

Figure 1. Dynamics of pre-disturbance and post-disturbance CWD patterns in a forest stand with time since disturbance (adapted from Sturtevant et al. (1997).

According to forest acts and other regulations in Europe, foresters have to follow certain prescriptions (e.g. Forest Stewardship Council – FSC) to leave CWD in managed forest. But what is a sufficient amount? The amount of dead wood in a natural forest depends basically on three factors: the fertility of the site, the decaying process of dead trees (influenced by position, species, microclimate, fungal decomposition) and disturbances which have effects on the mortality rates and patterns of trees (Harmon *et al.*, 1986; Jonsson, 2000; Siitonen, 2001). The formation of dead wood is largely driven by natural disturbance agents, like storms and wildfires (Harmon *et al.*, 1986; Samuelsson *et al.*, 1994). In natural conditions, recurring disturbances, either small-scale gap perturbations or large-scale stand-replacing catastrophic events (continuously but irregularly) replenish and create coarse woody debris (Kuuluvainen, 1994; Siitonen et al., 2000). The most drastic effect of a disturbance (tornado-like strong turbulent winds) can be the instant killing and felling of all trees over a large area.

In natural south and middle boreal forests in Fennoscandia, the amount of dead wood is reported between 20 m^3ha-1 and 120 m^3ha-1 (Linder *et al.*, 1997; Jonsson, 2000; Siitonen, 2001; Karjalainen and Kuuluvainen, 2002; Kuuluvainen, 2002). Pine-dominated forests have in general lower

CWD volumes than spruce-dominated ones (Kuuluvainen, 2002). In most studies it has been found that about 30 % of the total CWD volume is in standing dead trees and 70 % in down woody material and stumps. In pine-dominated forests the standing part of the total CWD-volume is usually higher than in spruce-dominated ones (Kuuluvainen, 2002). In Fennoscandia, intensive forest management has considerably reduced the amount of decaying wood (Siitonen *et al*., 2000). Regular thinning of stands, clearcut harvesting, efficient forest fire prevention etc. have all contributed to a general decrease in CWD in managed forests (Siitonen *et al*., 2000). Selectively logged/semi-natural stands have a high volume of CWD when compared with managed stands and almost the same volume of CWD as natural stands, but they can be poorer in decaying wood-associated (saproxylic) species than natural stands.

As an important agent creating habitat heterogeneity in time and space, windfall disturbance is one of the driving forces for forest succession as well as a source of regional biodiversity in forest ecosystems (Bouget and Duelli, 2004). Extreme wind can damage trees by uprooting them, snapping their trunks, or causing bending to occur, resulting in blowdown of canopy trees (Brassard and Chen, 2006). Wind-felled Norway spruce (Picea abies, L.) offers breeding ground for a wide range of insects and pests (Eriksson *et al*., 2005), which in case of more severe windstorms may lead to a population outbreak and subsequent attacks on living spruce trees (Schroeder, 2001). It is well known that large-scale outbreaks of the spruce bark beetle (Ips typographus L.) will develop when large numbers of fallen spruce trees are left in the forest after storm or other disturbances (Peltonen, 1999; Göthlin et al., 2000; Nageleisen, 2001; Hedgren *et al*., 2003; Meier *et al*., 2003; Okland and Berryman, 2004). Generally *I. typographus* prefers to reproduce in wind-felled or otherwise damaged trees, but in some situations it is also able to damage and kill living trees in large numbers (Schroeder, 2001). Salvage logging or retention of wind-felled trees and the risk of consequential tree mortality is an important problem in forestry practice (Duelli and Obrist 1999, Wichmann and Ravn 2001, Eriksson et al. 2007)

Now some countries have the goal of retaining biodiversity by leaving more wind-felled trees in the managed forest (Schroeder, 2001). There are regulations according to what we need to leave all disturbance damaged trees untouched in protected areas and preserves, therefore it is important to evaluate the risk of damage caused by the wind, by bark beetles and other factors, and for that we need easy, cheap and accessible data sources. There are different methods in use. Landscape photography from a single location is used to view the typical landscape features under different environmental conditions (Dahdouh-Guebas and Koedam, 2008). Some scientists have used sequential photographs to investigate ecosystem vegetation changes (Moseley, 2006). Various methods have been used to estimate the numbers of weakened, damaged or killed trees. In North America a sequential aerial photography method was used to detect trees killed by bark beetles (DeMars *et al.*, 1980). Panoramic photography has been used to estimate bark beetle-killed or drought-stressed trees and to investigate other forest damage types (Caylor *et al.*, 1982; Ciesla *et al.*, 1982; Dillman and White, 1982; Klein, 1982). Recently roadside sampling was used to assess bark beetle damage in France (Samalens *et al.*, 2007). A new possibility is to use repeat photography for such estimations.

2.2. CWD decay dynamics

Previous studies 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 have different severities and generate 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 should be studied in both closed forest and open areas. Factors that control decomposition in these areas, such as temperature, moisture, light conditions, organisms involved, can vary significantly and decomposition in areas with initially comparable conditions but with a different damage severity can be completely different (Harmon *et al.*, 1986; Storaunet and Rolstad, 2002). Decay characteristics have important implications for seedling establishment. In spruce forests, once the sapwood rots and bark falls off, available nutrients may provide ideal conditions for the establishment and growth of seedlings (Brassard and Chen, 2006).

2.3. Regeneration

In at least two recent conceptual models of forest disturbance and recovery, those of Frelich, (2002) and Roberts (2004), severity is one of the primary axes to differentiate disturbance effects. Disturbance severity determines which component of pre-disturbance vegetation survives or is killed. In the same time disturbance intensity refers to the amount of energy released by the physical process of disturbance. In case of windstorms, intensity and severity are highly correlated. Consequently, severity can influence regeneration in two ways: (1) the physical change in light and nutrient availability; (2) the availability of seed trees, seedbanks or advance regeneration for seedling establishment. By inducing higher light levels, changing the soil and liberating space, storm-damaged areas promote the density and diversity of understory vegetation and regeneration (Bouget and Duelli, 2004). Both early-successional (Kuuluvainen and Juntunen, 1998) and late-successional trees have been shown to recruit in openings created following blowdown (Brassard and Chen, 2006).

Regeneration via seed in storm-damaged areas depends on patches suitable for germination, establishment, and survival (Ulanova, 1998; Ruel and Pineau, 2002). Environmental conditions within the gap vary greatly, and can positively or negatively influence each of these stages. Light availability, for example, increases most north of the gap center, in the northern hemisphere, (de Chantal *et al.*, 2003), which could alter the community structure (Hytteborn and Packham, 1987; Dyer and Baird, 1997; Drobyshev, 2001). The increased light levels in the small gaps available in the multi-layered forest provide early establishment opportunities for seedlings, but by the time the nutrients become available, these gaps are filled already by the neighbouring canopy trees or advance regeneration (Lundqvist and Nilson, 2007).

Many tree species (including spruce) have a tendency to be uprooted instead of breaking at the bole, creating ideal regeneration conditions (Brassard and Chen, 2006). Uprooted trees increase environmental heterogeneity because of the creation of a pit–mound microtopography by the relocated root systems and because of the freed space on the forest floor (Ulanova, 1998, 2000). Pits, defined as the areas where mineral soil has become exposed, mounds, defined as the rootplates that have turned into a vertical position, intact forest floor and decaying logs provide areas with very different microclimates and conditions (Peterson and Pickett, 1990;

Peterson and Pickett, 2000; Ulanova, 2000; Ruel and Pineau, 2002), which in turn may increase biodiversity at the stand level (Lässig and Mocalov, 2000).

2.4. Research needs

There is a general lack of knowledge of dead wood dynamics after catastrophic disturbance in forest ecosystems. The role of CWD in providing habitats and carbon cycling is generally understood; perspectives on its role in nutrient cycling and regeneration are still evolving. It is often stated by many authors, that CWD is critical to site fertility and productivity, serving as long-term source for nutrients that protects the ecosystem from disturbance-related nutrient losses (Harmon et al., 1986; Siitonen et al., 2000; Laiho and Prescott, 2004). However the nutritional importance of CWD in this regard, relative to other types of debris, has rarely been assessed. Also the time it takes before nutrients leach out from woody material and whether this has a positive effect on regeneration, have rarely been investigated. Further complex studies, that are trying to give wider perspect (as shown in figure 2) of CWD dynamics after disturbance, are needed.

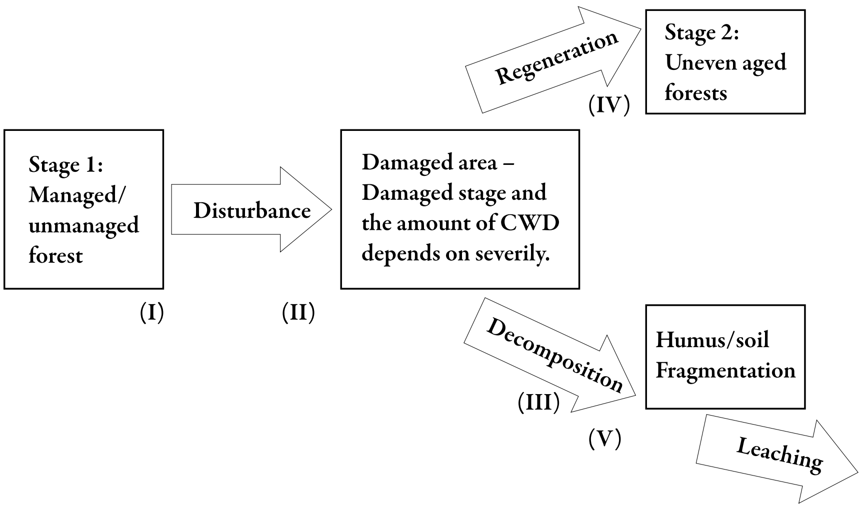

Figure 2. Changes within ecosystem after disturbance. Disturbance severity determines the damage stage (completely damaged, or damaged to some extent), which in turn influences the regeneration of the area and decomposition processes (including nutrient dynamics) in the area. The Roman numbers are referring to the published papers.

Also the question of how much CWD is required in forests to ensure and sustain ecosystem functions is open. Today this has been solved by the application of static minimum standards based on a set of general objectives, but in the future a more dynamic and specific objective-oriented approach should be developed. We need detailed understanding on how certain species and ecosystem processes vary with the amount of CWD. An important management question after windstorms is whether to leave or harvest the windthrown trees. General forestry practice prescribes salvage harvesting after heavy storm damage because of the fear of insect outbreaks and fire hazard. But not all trees have the same economical value or the same value for biodiversity, thus guidelines that promote biodiversity and minimize economical loss could be developed. This concerns stand level, where parts of trees and already damaged trees could be left instead of whole healthy and valuable trees (Jonsson and Kruys, 2001).

3. AIMS OF THE STUDY

The aims of the present doctoral thesis were:

1. 1. To describe the CWD (status) in formerly managed and untouched (minimum 60 years without interference in the course of the last century) stands in two Estonian national park forest ecosystems (**I**);
2. To evaluate tree mortality after windthrow at the edge of a heavily disturbed forest area, how big are bark beetle damages couple of years after wind-disturbance (**II**);
3. To examine 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 windthrow areas in east Estonia (initially similar areas damaged to a varying extent) (**III**; **V**);
4. To find out how disturbance severity and management influence recovery of regeneration (**IV**);
5. To detect changes in CWD nutrient concentrations and in soil nutrient content and also to examine how the disturbance severity and soil nutrient content influences recovery of regeneration (**V**).

4. MATERIAL AND METHODS

4.1. Study areas

The original studies (**I-V**) were carried out in Estonia, in the hemiboreal vegetation zone (Ahti *et al*., 1968), where the average temperature is +5.2 °C. The coldest month is February, with -5.7 °C and the warmest month is July, with +16.4 °C. The average precipitation is 550-650 mm.

The data of this thesis was collected from four separate areas: the study areas on variation and ecological characteristics of coarse woody debris (**I**) were situated in North Estonia in Lahemaa National Park (59°31' N 25°90' E) and in South-East Estonia in Karula National Park (57°43' N 26°35' E) (Figure 3). A national park may belong to one of the following protection categories: strict nature reserve, special management zone and restricted management zone. Usually these three categories are represented within the whole area, to ensure the most effective protection of biodiversity. Lahemaa National Park was established in 1971. The area of the national park is 725 km^2, of which 474 km^2 is land and 251 km^2 is sea. Citizens today privately own 60% of the forests in the park. Certain areas of this national park, belonging mainly to the special and the restricted management zones, are partly managed by traditional methods.

The main conifers in the study area were Norway spruce (*Picea abies* (L.) Karst.) (38% of the stands) and Scots pine (*Pinus sylvestris* L.) (34% of the stands). Birch (*Betula pendula* Roth. and B. *pubescens* Ehrh.) (20% of the stands) and black alder (*Alnus glutinosa* (L.) J. Gaertn.) (8% of the stands) were the most common deciduous trees. The average age of the studied stands was 80 years, with a range of 40 – 200 years. Coniferous-dominated forests are considered mature after 90 years and deciduous-dominated areas after 75 years in Estonia.

The Karula National Park was created in 1993 and since 1979 it was a landscape reserve, which means that more intensive management was allowed. Being the smallest National Park in Estonia it covers 11 100 ha and it was created to protect the typically South-Eastern Estonian forest and lake rich landscapes. The main tree species in the study area were Scots pine (75% of the stands), Norway spruce (14% of the stands) and birch species (17% of the stands). The average age of the studied stands was 75 years and varied from 20 – 160 years.

Figure 3. Location of the sample areas in Estonia, representing (a) Lahemaa National Park, (b) Karula National Park, (c) Tudu windthrow area and (d) Halliku windthrow area.

The areas for the assessment of tree mortality, effects after forest disturbance in decomposition of trees and regeneration development studies (**II-V**) were located in the former Tudu Forest District (59°11' N 26°52' E) and in the former Halliku Forest District (58°43' N 26°55' E) in Eastern Estonia (Figure 3), which experienced severe windthrow on 16 July 2001 and 5 July 2002, respectively. 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.). The study areas include stands on Eutric Gleysols and Calcaric Cambisols (FAO et al., 1998; Reintam *et al*., 2001), *Filipendula* and *Myrtillus* forest site types (Lõhmus, 1984) being most commonly represented. Formerly the forests were under protection (landscape preserve), meaning that they have been unmanaged for decades. The stand ages ranged from 110 to 160 years.

4.2. Field and laboratory measurements

In Lahemaa and Karula National Parks (**I**) we selected two areas with different management histories: a strict reserve and a managed area only selective cutting have been carried out for centuries). In total 304 sample plots, 134 in Lahemaa and 170 in Karula, with an 11.28m radius (0.004 ha) were randomly selected for dead wood inventory. The area under study in Lahemaa was 141 ha and the total area of sample plots was 5.36 ha (3.8 % of the total, regarding both strict nature reserve and managed areas). The area in Karula was 158.6 ha (different management histories) and the total area of sample plots was 6.8 ha (4.3% of the total, regarding both strict nature reserve and managed areas). The inventory took place in the summer of 2001. As the areas have been not managed at all or only selective cuttings have been carried out the main factor creating dead wood in the area has been small-scale disturbances that creates gaps. We used the areas to get the reference status of dead wood in pre-disturbance conditions. The sampling unit in managed and unmanaged areas was the forest stand. In case of spruce and pine stands, we used all the stands that were older than 90 years and in case of birch and black alder, we included all stands that were older than 75 years. Inside each stand (uniform forest subcompartment with a size larger than 0.1 ha) we located one sample plot randomly. In stands with an area less than 1 ha one plot was established, in larger stands two or even three to four sample plots were established. In each plot we measured all standing and laying dead wood with diameter >10 cm in the thinner end. For standing dead trees (min. height 1.3 m) the following variables were recorded: tree species, diameter at breast height, height of the tree/snag and decay stage divided into five groups. For laying dead wood the following variables were recorded: tree species, diameter at both ends of stumps (at the base and at the top), decay stage divided into five classes and the way of falling (natural or cut). In case of stumps we measured all stump diameters and decay stages, but we separated natural stumps from man-made, where it was possible. The Estonian forest management site index classification system (Krigul, 1971) was used to describe stand quality and productivity of the site. The site type, age, standing stock and management history data were taken from local forestry inventory databases.

In Tudu and Halliku areas (**II-V**) where storm caused formation of dead wood fieldworks were conducted in the summers of 2003, 2004, 2005 and 2006. Data from 12 study plots (40 m long x 20 m wide) were used. The study plots were located in areas of four different disturbance severity classes – (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 (canopy of living trees) and (iv) areas that were logged (LG) after wind damage (harvested). The heavily and moderately damaged study plots were established in protected compartments (dead wood was left on site); and the logged plots were in surrounding managed forests of the Tudu and Halliku Forest Districts. Each "treatment" had four replicate transects. The plots were established one year after the storms.

For studying the tree mortality after windthrow (**II**), photographs were taken from three completely damaged areas with total canopy destruction. A Nikon D50 digital single-lens reflex camera with 6.1 million pixel elements was used to capture the images. The camera location and photo point remained the same, as we used permanent markers for that purpose. The first picture was taken at the end of January in the winter of 2002, six months after disturbance. This photo image is regarded as the initial stage of measurements. Local observations were carried out to visually determine the causes of mortality. In the first picture, we numbered every spruce that we could distinguish on the image and later verified what changes took place in subsequent years. Multiple observers worked with the first picture until all of them got the same tree count. We placed each tree into one of four classes in every year: living tree – tree shape and crown not damaged; standing dead tree – with no needles detected; damaged tree – at least 25% decrease in crown density; fallen tree – disappeared from picture. In total 137 spruce trees were observed during the five-year period.

For studying the decomposition processes (**III**) 334 sample logs and snags were analysed (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 laying or leaning) were randomly selected among spruce (*Picea abies* L. Karst) and birch (*Betula* spp.). Only logs and snags with >10 cm in diameter and > 1.3 m in length/height were sampled. 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 in order to get four wood subsamples). The outermost diameters, longitudinal and radial thickness of bark were measured at two points on each disk (where the values were highest and lowest, as assessed visually). The bark was removed from the wood and the wet mass of each sample was determined (with precision 1g). Wood subsamples (ca. 20g) were taken from each disk, weighted and air-dried in paper bags to stop decomposition. The cores were taken from different locations on the disk depending on its diameter (Figure 1 in **III**). The data set for analyses included a total of 944 subsamples from 174 spruces and 160 birches.

The dry mass of the cores was measured after oven drying at 65 °C to the constant mass (precision 0.01g). 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 g cm^{-3}, the weight of the displaced water equals the volume of the sample. The basic density (d, in g cm^{-3}) of each sample was calculated by the equation

$$\mathbf{d = m_0/V} \tag{1}$$

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

At the same time sample trees for wood nutrient concentration measurements (**V**) were selected from permanent sample plots. In total we analysed 58 sample logs, snags and living trees, from where we were taking 134 wood samples of two tree species (spruce and birch). N, P, K content of the wood was analysed to determine the changes in wood nutrient content.

For analysing soil nutrient concentrations (**V**) 4 soil samples were taken from each sample plot. Soil samples were linked with those ten undamaged forest floor squares used for regeneration survey and taken randomly from the other side of the transect. Samples were taken from depth 5-15 cm and analysed in laboratory to find N, P, K content of the soil and pHKCl.

The regeneration surveys (**IV**) were performed in two subsequent years (autumn 2004 and autumn 2005) in pits, on mounds and on ten 1 m^2

quadrates, which were established on undamaged forest, floor along the middle transect of each study plot. The species of uprooted tree was recorded, its mound width and pit depth was measured with a measuring tape. The perimeter points of pits and mounds and locations of seedlings were mapped using a surveyor's compass and electronic distance and height meter Vertex III (Haglof, Inc.) and the areas of pits and mounds were calculated using the formula of circle sector area to calculate the density of seedlings.

The number of tree seedlings was recorded by species. The tree seedling height was measured. Height increment was calculated as the difference in height in successive surveys. Location (pit, mound or undamaged) and species were determined. Based on visual survey, pre- and post-disturbance seedlings and sprouts were separated, and only data from seedlings established after the storm were used in statistical analyses. Seedling density was found by dividing the tree number by the area of the microsite (bit, mound, square). The result was categorized into three density classes (I class < 5 seedlings, II class < 10 seedlings; III class ≥ 10 seedlings). The pre-disturbance regeneration comprised approximately 7% of all regeneration trees in moderately and heavily damaged areas in 2004. When only regeneration trees on intact forest floor were considered, the given proportion was 27%.

4.3. Data analysis

Conventional parametric statistics (ANOVA, GLM) (**I, III, V**) and non-parametric statistics (Kruskal-Wallis ANOVA, chi-square (χ^2) test) (**II, IV**) were used for hypotheses testing.

In three papers (**I, III, V**) main statistical analyses were carried out with the SAS procedure 'Mixed' (Release 9.1). This procedure realises the general linear mixed model analysis, which enables one to test whether, and how, the different factors are affecting each other.

For assessment of tree mortality after windthrow (**II**), we used a transition matrix (Eq. 2) to determine the probabilities with which trees in different classes moved to another class. This matrix was then of the form:

$$A = \begin{pmatrix} p_{11} & p_{12} & p_{13} & \cdots & p_{1n} \\ p_{21} & p_{22} & p_{23} & \cdots & p_{2n} \\ p_{31} & p_{32} & p_{33} & \cdots & p_{3n} \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ pn_1 & pn_2 & pn_3 & \cdots & pnn \end{pmatrix} \tag{2}$$

where p_{1n} was the probability of transition to class 1 from n time intervals. Multiplication of this matrix, A, by a column vector x(t) that describes the tree state class at time t, gives the tree state class at time t + 1.

In regeneration survey (**IV**) Kruskal–Wallis ANOVA was performed first to find the effect of disturbance severity and microsite on seedling density. The Mann–Whitney U test was then performed on seedling densities among microsites to test for pairwise species microsite preference. Nested ANOVA was used to determine the influence of study plot, soil type, storm year, damage severity, microsite and recruitment tree species on increment. Later the one-way ANOVA was used to examine the influence of microsite, pooled seedling density classes on microsite and density classes of particular species being studied and theTukey test were used to find differences within the factor groups.

The programs Statistica 6 (StatSoft, Inc.), SAS software (version 9.1; SAS Institute, Cary, NC) and MS Excel (Microsoft, Redmond, WA) were used for data analysis.

5. RESULTS

5.1. CWD status in managed and unmanaged forests as a reference for natural site

Different management history influences the amount and diversity of CWD (**I**). ANOVA demonstrated, that in areas where there has been no management the amount of CWD is significantly greater ($p=0.0404$) than in areas, where there have been occasional silvicultural operations (selective cuttings).

The CWD volume was significantly affected by standing stock volume, site index, site type and age (Table 4 in **I**). In each national park main determinants of CWD volumes were different. In Lahemaa, the factors having the strongest influences on amount of CWD were stand age ($p=0.008$) and site index ($p=0.02$). In Karula, the most important factor affecting the amount of CWD was standing stock ($p=0.02$). No significant difference in total CWD volume was found between Karula and Lahemaa (Table 5 in **I**).

The CWD volume increased significantly with stand age in the studied areas (Table 4 in **I**). The partition of the stands into age classes clearly revealed, those with increase of age, both the amount of standing stock and CWD are increasing until a certain age (Figures 2 and 3 in **I**). In mature stands, the volume of standing stock, as well as CWD, did not change with age.

The volume of CWD did not depend on the site type (Lahemaa $p=0.09$; Karula $p=0.37$) nor on dominant tree species (Lahemaa $p=0.65$; Karula $p=0.07$). However there were some tendencies, but these were not statistically significant. In Karula, where pine was the dominant species in CWD (76% of measured stands were pine dominant), standing CWD volume exceeded usually fallen CWD (Figure 4 in **I**). In Lahemaa the opposite tendency was observed in first three site index classes due to Norway spruce dominance. In the IV and V site index classes, which were mostly dominated by pine, the volumes of standing CWD and fallen CWD were almost equal (Figure 5 in **I**).

5.2. Tree mortality after windthrow in surrounding areas

During a five-year period, approximately 25% of the spruces survived in areas surrounding the windthrow. On average, per plot only 11 trees out of 35 survived (Figure 2 in **II**). The largest number of damaged/suffering trees (more than 22% on average) was found in the second year after disturbance (Table 1 and Figure 2 in **II**). The transition probability matrix (Table 1) demonstrated that most of the damaged trees died during the second year after disturbance, but some recovered.

Table 1. Transition probability matrices. The columns represent transitions from each class initially at time t, while the rows represent transitions to each class one time interval later (t+1). Class group codes are: 1 - living tree; 2 - damaged tree; 3 - fallen tree; 4 - standing dead tree.

	1	**2**	**3**	**4**
Number of trees in 2002	105	5	0	27
2002-2003 $p<0.0001$				
1	0.277	0.000	0.000	0.000
2	0.204	0.015	0.000	0.000
3	0.044	0.000	0.000	0.036
4	0.241	0.022	0.000	0.161
2003-2004 $p<0.0001$				
1	0.248	0.036	0.000	0.000
2	0.015	0.058	0.000	0.000
3	0.000	0.007	0.073	0.007
4	0.015	0.117	0.000	0.372
2004-2005 $p<0.0001$				
1	0.219	0.036	0.000	0.000
2	0.036	0.022	0.000	0.000
3	0.015	0.007	0.131	0.124
4	0.015	0.007	0.000	0.387
2005-2006 $p<0.0001$				
1	0.219	0.036	0.000	0.000
2	0.007	0.015	0.000	0.000
3	0.007	0.000	0.277	0.073
4	0.022	0.007	0.000	0.336

Note: Differences between matrices were tested by chi-square (χ^2) test.

The most rapid change in the number of living trees took place during the second year after disturbance (Figure 2 and Figure 4 in **II**), but a remarkably high recovery of damaged trees was observed every year. The number of standing dead trees increased till the third year after disturbance (Figure 2 in **II**), later the number decreased as these trees started to fall down. Table 1 shows that the probability of a standing dead tree falling down was greatest at the end of the fourth year, but in general a considerable number of standing dead trees fell each year.

5.3. Dynamics of CWD decomposition

A mean CWD density decrease, both in spruce and birch, was observed 2-3 years after disturbance. Damage severity had a clear correlation with the CWD wood density at the end of three-year period (Table 2). In more damaged areas the density of wood was lower than in less damaged areas (it applies for both tree species). The results of our study revealed that the wood decomposition (wood density changes) also depends on log or snag position (Table 2). Ranking wood density by log or snag position we found out that laying logs were decomposing faster than leaning logs and standing snags (Figures 2 and 3 in study **III**).

As the stage 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 since the damage. Row 11 of Table 2 shows that the effect of time may be real but row 10 still leaves open a possibility that, due to imbalanced data, this effect may indirectly be caused by tree species, forest habitat properties and snag/log position. The 3-year decay period is too short to estimate the long-term decomposition rate.

We also investigated how the core position on the sample disk influenced CWD density. This factor was represented 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 2, Row 7). At the same time the random factor was significant for spruce (Table 2, Row 9). The structure of the covariance applied AR(1) had a significant negative correlation parameter ρ ($\rho = -0.37$, $P = 0.0044$, Table 2, Row 9). The minus sign means that when moving from the upper margin of the spruce core disk to the lower margin, a wavy density change could be observed.

Table 2. 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 or totally damaged, Snag/Log position – laying, leaning or standing, Disk position – position of the sample disk on the trunk (three positions for a tree), Core position – position of the core sample on the sample disk (see Figure 1 in **III**), 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 of the residual variance of dependent variable may differ. $\sigma^2\varepsilon$ and ρ are parameters of the covariance structure AR(1) characterizing dependence between the four cores on the sample disk (Figure 1 in **III**): $\sigma^2\varepsilon$ is the residual variance of LDensity and ρ is the correlation between the adjacent cores on the sample disk. 'Major factors in Type I Analysis' 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 calculations.

No	Factor No	Factor (type)	Nested/GroupedWithin	DF	ANOVA Type or Covariance parameter	Major-factorsin Type I Analysis	P-value
1	0	Tree (R)	1	–	$\sigma2\varepsilon$=0.013	–	< .0001
2	1	Species (F)	–	1/188	I, III	–	< .0001
3	2	Region (F)	–	1/188	I, III	1	n.s.
4	3	Damage (F)	–	2/188	I, III	1, 2	< .0001
5	4	Snag/Log position (F)	–	2/188	I	1	< .0001
6	4	Snag/Log position (F)	–	2/188	III	–	n.s.
7	5	Core position on disk (F)	1, 4	14/188	I, III	1, 2, 4	n.s.
8	6	Core position: birch (R)	0, 1	–	AR(1)	–	n.s.
9	6	Core position: spruce (R)	0, 1	–	AR(1), ρ = −0.37	–	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	< .0001
12	8	Disk position (R)	0	–	–	–	0.0104
13	8	Disk diameter (F)	–	1/188	I, III	1–4, 6, 7	0.0312

5.4. Regeneration after windstorm

Species composition of seedlings differed in areas with different damage severity and among microsites (Table 3 in IV). The Shannon diversity was highest in areas with moderate damage, followed by heavily damaged areas. The least diversity and evenness were found in harvested plots, where birch strongly dominated (Fig. 2 in IV). Pits showed the highest diversity among microsites. Species were also more evenly distributed in pits. The damage severity had significant influence on pooled total seedling density and densities of aspen, birch, spruce, alder and rowan (Kruskal–Wallis tests, $p < 0.001$ in all cases). The pooled total seedling density and density of aspen seedlings were higher in harvested plots than in heavily damaged and moderately damaged plots. The density of birch was highest in harvested plots and lowest in moderately damaged plots. Spruce was least abundant in harvested areas (Figure 4).

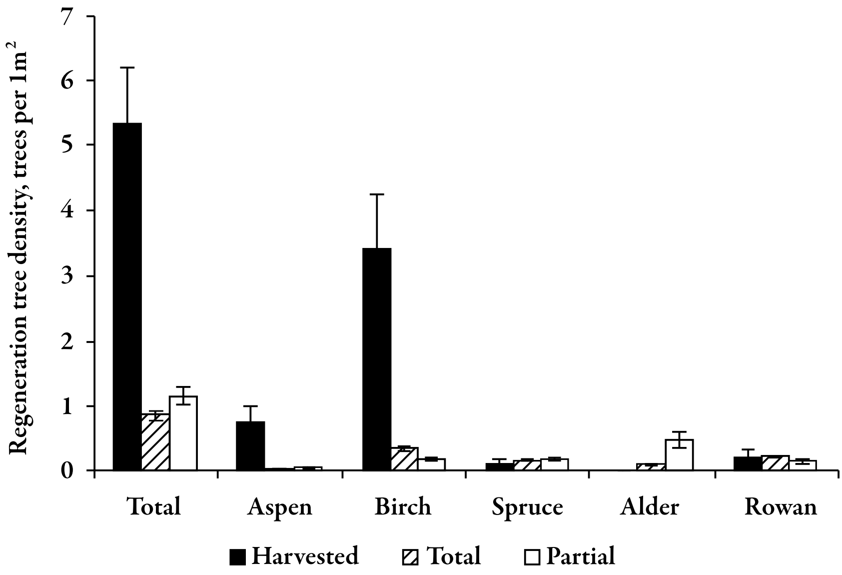

Figure 4. Mean regeneration tree densities in areas with different damage severity in 2004.

Microsite significantly affected pooled total densities (Kruskal–Wallis tests, $p = 0.0055$), as well as the densities of birch ($p < 0.001$) and alder ($p < 0.001$) (Fig. 4 in IV). The pooled total seedling density was the lowest on mounds compared to pits and intact area. Birch had highest seedling densities in pits. Alder was mostly in pits as well, only 8 trees being found on intact ground. Seedlings of other species did not show any preferences among microsites.

There was no significant influence of transect, damage severity, soil type or storm year on recruitment tree growth, but microsite and tree species showed significant influence (nested ANOVA, see Table 4 in IV). The incremental growth of birch and rowan was significantly greater with lower seedling density. Birch was most dense on mounds as against intact areas and pits, while rowan was least dense on intact areas (one-way ANOVA, see Table 5 in IV).

Survival of recruitment trees was influenced by seedling height and seedling species (logistic regression, $p < 0.001$ in both cases). Birches surviving to 2005 were significantly taller in 2004 than those that died by 2005 ($p < 0.001$). Surviving birches were also taller on gleyed podzolic soils ($p = 0.0187$) and on areas where birch seedling abundance was lower ($p = 0.0354$). Survival of spruce did not depend on tree height, but the height differed among microsites ($p = 0.0024$). The tallest spruces were found on intact microsites and the shortest were in pits. Spruces were also taller in heavily damaged areas than those in moderately damaged areas ($p = 0.0406$). Surviving alders were taller in heavily damaged areas ($p < 0.001$), on gleyed soils ($p < 0.001$), with lower total seedling abundance ($p < 0.001$) and with lower alder seedling abundance ($p < 0.001$). Rowans and aspens surviving to 2005 were only significantly influenced by tree height ($p = 0.0081$ and $p < 0.001$ respectively). Those that were taller in 2004 had more chance of surviving to 2005. Pit depth and mound thickness differed among uprooted species (Kruskal–Wallis tests, $p < 0.001$ in both cases). Uprooting of Norway spruce created the shallowest pits and thinnest root plates (Fig. 5 in IV). No significant differences in the numbers of seedlings on different uprooted tree species were found, although a slight trend for hardwood mounds to have more seedlings than spruce mounds can be observed. In general, seedling abundance was relatively low on mounds. From the point of view of stand development in the future the site fertility is important. More fertile sites (Filipendula site type in our case) have a greater potential of natural regeneration in totally damaged and especially harvested plots (Figure 4 in V), where greater amount of N, P and K in the soil had positive influence on total density and density of birch and Norway spruce. But in general, 3-4 years after disturbance there were no changes in nutrient concentration of CWD in windthrow areas.

Also the N, P, K content of soil profile showed no significant difference between areas with different damage severity inside the site type, but it differed between Myrtillus and Filipendula site types (Figure 3 in V). The concentration of three main nutrients (N, P, K) stayed stable. When talking about CWD then in partly damaged areas and in totally damaged areas the laying and leaning dead trees showed changes in nutrient concentrations (decrease, increase) but no trends have become (or were) visible. Standing snags on these areas showed almost no changes in nutrient concentrations when compared with living trees.

6. DISCUSSION

The dynamics and amount of CWD are different in natural and managed stands. The amounts in managed stands are usually low compared to amounts produced by natural disturbances. In old stands the importance of mortality caused by senescence and small-scale gap disturbances increases with stand age. The short-rotation periods in managed forest reduce this development before large-diameter dead trees start to accumulate. In unmanaged, natural old forests, the amount of CWD stays stable. Because the largest (in diameter) CWD is the most valuable local resource in the coniferous forests in the long run, protected areas are extremely valuable as reference areas and core areas.

In reserves (in unmanaged areas) there is a considerably higher amount of CWD than in protection zones (buffers around strict nature reserve which have been occasionally managed). Areas in Lahemaa, which have been clear-cut at the beginning of the 20th century, had a much lower volume of CWD than areas, which were thinned. In areas that were not managed the amount of CWD is on the same level as in areas, where there have been selective cuttings. The low CWD volumes in managed forests (14.1 m^3ha^{-1} in Lahemaa and 10.6 m^3ha^{-1} in Karula) are typical for managed forests, because silvicultural thinning reduces mortality by self-thinning and the recruitment of dead trees (Rouvinen *et al.*, 2002a). The main factor affecting the amount of CWD in studied stands was the volume of living trees (standing stock), which is in accordance with earlier studies in northern Europe (Linder *et al.*, 1997; Siitonen *et al.*, 2000; Köster *et al.*, 2003). Standing volume is, in turn, highly influenced by site productivity and the age of the stand (Siitonen *et al.*, 2000; Krankina et al., 2001; Köster *et al.*, 2003).

The results of this study are consistent with other studies of CWD stores in similar managed and unmanaged ecosystems. For example in southern Finland the CWD volume in mature and overmature silviculturally managed forests was 14.4 m3ha-1 and 23.3 m3ha-1, respectively (Siitonen, 2001). In Russia, in the St. Petersburg region, the volume of CWD in mature and overmature forests was 24 m^3ha^{-1} (Krankina *et al.*, 2002). In natural or seminatural forests in the southern boreal forest zone the amount of CWD can be much higher, from 70 to 184 m^3ha^{-1} depending on the successional stage of the stand and on the input rate caused by disturbances (Siitonen *et al.*, 2000). In north-western Russia, virgin taiga forests, the proportion of CWD can be as much as 35–40% of the total volume (Kuuluvainen *et al.*, 1998). In general, the higher the natural tree volume is, the greater is the amount of CWD in natural forests.

In the published CWD studies made in Estonia, Kasesalu, (2001) measured CWD in a small-sized (19.3 ha) old protected area in Järvselja (in East-Estonia) and found that on average CWD amounts were great: 98.99 ± 59.7 m^3ha^{-1} (23 % (9 - 40%) of the total stand volume). In Alam-Pedja National Park in Central Estonia Lõhmus and Lõhmus, (2001) found that amounts of standing CWD were 21 m^3ha^{-1}. In our study the volume of CWD was on average 48.5 m3ha-1 in Lahemaa and 27.6 m^3ha^{-1} in Karula. The percentage of CWD from total timber volume was on average 21% in Lahemaa and 15% in Karula.

It is important to evaluate the risk of damage caused by wind, bark beetles and other factors. Salvage logging is a decision often made by managers after disturbance because of the fear of insect outbreaks and fire hazard (Stanturf *et al.*, 2007). Many large-scale outbreaks of spruce bark beetles have been reported in Estonia over the last two centuries, in 1868-1874, 1880-1886, 1897-1902, 1912-1915, 1924-1929, 1934-1940, 1968-1973, and 1992-1995 (Voolma, 1998; Voolma et al., 2000; Wichmann and Ravn, 2001; Voolma, 2002). Various natural disturbances in forests have usually preceded the outbreaks: a hot summer and big forest fires in 1868, snow breaks in 1879-1880 and 1911, storm damage in 1923, 1938, 1943, 1967 and 1969, and drought in 1882, 1934-1935 and 1992.

The results of our study followed the same pattern as reported in earlier papers, in which the mortality in the surrounding areas of heavy windthrow was highest in the second or third summer following the storm disturbance (Schroeder, 2001; Bouget and Duelli, 2004; Eriksson *et al.*, 2007). Almost half of the tree deaths were recorded in the second year following the wind felling. These tree deaths were probably caused by I. *typographus*, as it came out from local observations that all the dead spruce trees were colonized by it.

Some studies found that in very hot summers, as in 2001 and 2002, I. *typographus* prefers the cooler inner parts of the stands for breeding rather than sun-exposed open habitats (Eriksson *et al.*, 2007). Bark beetles generally prefer wind-felled or otherwise damaged spruce trees (Schroeder 2001, Eriksson *et al.*, 2007), but most wind-felled trees become unsuitable as breeding-ground a year or two after disturbance (Bouget and Duelli, 2004) and bark beetles are confined to attacking living trees on the surrounding edges (Peltonen 1999, Schroeder 2001).

The probability for both dead standing and living trees to fall down was surprisingly high during the entire five-year study period. It usually takes some decades for standing dead trees to fall because of decomposition (Storaunet and Rolstad, 2002; Storaunet, 2004; Storaunet and Rolstad, 2004), mainly because of drying out after death (Krankina and Harmon, 1995). This quite early falling of standing dead trees implies that not all spruces were killed by bark beetles. Here we can consider the co-influence of various disturbance types. The root systems of living spruces were probably damaged by storms or fungi, thus weakening the trees. Bark beetles killed the trees and these standing dead spruces fell so early because of their damaged root system. The co-influence of storm damage and bark beetle attack made the trees die quickly and they blew down with the next strong winds. It is also possible that other factors besides partial damage and associated bark beetle attack are responsible for tree death. An altered water regime or temperature fluctuations in open conditions may increase susceptibility to bark beetle attack or infection by fungi (Harmon *et al.*, 1986; Storaunet and Rolstad, 2002; Storaunet, 2004; Storaunet and Rolstad, 2004).

The input of CWD varies spatially on a number of scales. Within a stand, mortality may be aggregated or distributed randomly or regularly (Figure 5). Windthrows, insects and diseases, affect patches of trees and exhibit high contagious spatial patterns, therefore CWD generated by these factors can be expected to be aggregated (Harmon *et al.*, 1986). 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 and it is at its lowest in mid-successional stages (Figure 5). As the stand develops (during succession), CWD volume resulting from annual mortality increases, first mainly due to competition and self-thinning, and later because of exogenous disturbances (Siitonen, 2001). In partly damaged areas the total volume of CWD is not declining after disturbance, it will increase during some years after disturbance (Figure 5), because some trees, that survived the initial disturbance, are weakened by damages and will die later. Finally death is caused by other factors, such as insects, fungi *etc*.

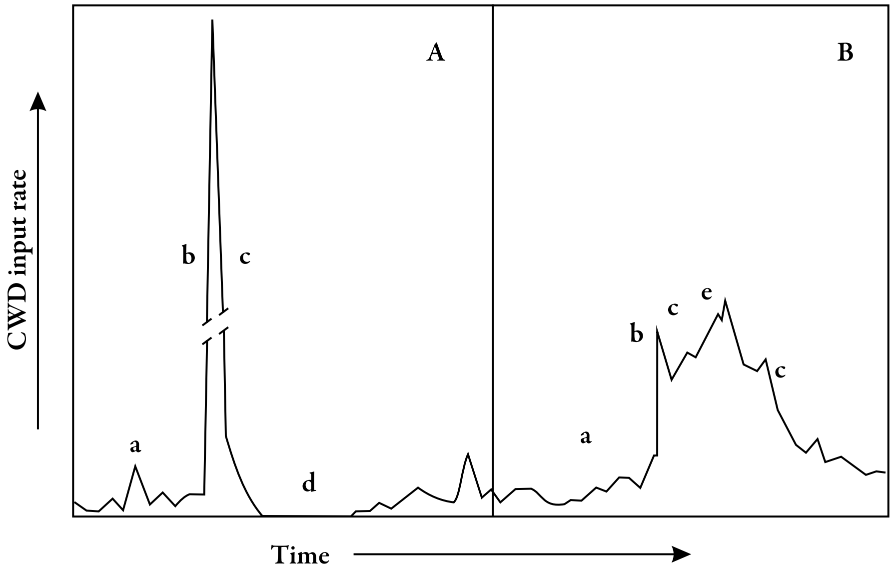

Figure 5. Changes in CWD input range over time in areas with different damage severity, where A represents totally damaged area and B represents partly damaged area. (a) represents minor annual input rate along long-term mean. (b) Represents large, rapid, but temporary increase in CWD input rate caused by disturbance. (c) Declining input rate as injured trees continue to die for a period after disturbance. (d) Initial lack of input followed by increase of input during the forest succession. (e) Gradual increase of CWD input associated with insect outbreak following the disturbance (adapted from Harmon *et al*., 1986).

Decay rates and density changes are different for different tree species (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. Deciduous trees in the boreal zone generally are decaying faster than coniferous trees. At the beginning of the decay processes, laying logs were decaying faster than leaning logs and remarkably faster than standing snags, thus disturbances creating snags increase overall turnover time of CWD. Felling makes wood available for colonization under conditions that are relatively non-stressful (Boddy, 2001). Also contact with the soil improves moisture level inside the log. Hytteborn and Packham (1987), and Naesset (1999) found that the decay rate (density loss) for spruce logs is most rapid when the logs are in direct contact with a moist forest soil. Naesset (1999) also found that in case of spruce the plots subject to limited solar exposure showed the most rapid decomposition, meaning that logs will decay faster in closed forest stands than in open areas. From our study it appeared that at least at the beginning of the survey decay processes in TD areas (open areas) were faster than in PD areas (stands with closed canopy). The reason here can be that after disturbance in TD areas the transpiration capacity of trees is low or is absent and the areas will become wet. So as the moisture level stays high, the wood material is not drying/seasoning through and in these warm and moist conditions are preferential for colonization of the wood material by decay affecting organisms (fungi). The loss of CWD volume is slower than the loss of CWD mass, at least in the beginning, because the density of dead wood declines before fragmentation starts to reduce the volume (Harmon *et al*, 2000; Laiho and Prescott, 2004). This implies a lower decay rate for volume than for mass (Siitonen, 2001). Disturbances affect biomass by adding CWD. It is possible to construct models predicting the CWD amount at different successional stages (outcome) (Figure 6).

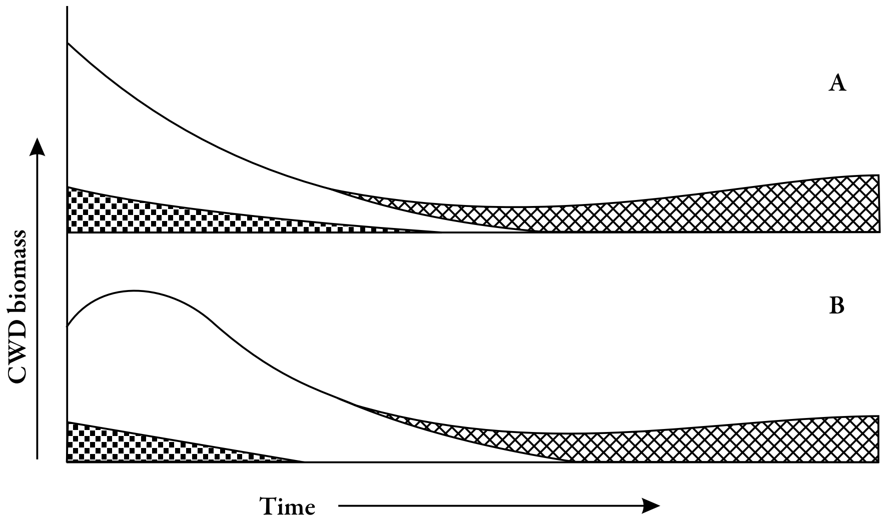

Figure 6. Hypothetical patterns CWD mass following disturbance, where A represents totally damaged area and B represents partly damaged area. CWD is divided into that present before disturbance (dotted), that created by disturbance (open) and that added by the stand growing after the disturbance (crosshatched) adapted from Harmon *et al.*, 1986 and Siitonen 2001).

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. The pits, mounds and intact forest floor can vary greatly in nutrient level, soil moisture, light and temperature (Peterson and Pickett, 1990; Peterson and Pickett, 2000; Ulanova, 2000; Ruel and Pineau, 2002), which implies greater species diversity in uncleared areas, as confirmed in our study. The harvested plots exhibit the highest degree of disturbance. Harvesting machines seriously damage the ground and hence the forest vegetation (Small and McCarthy, 2002).

The seedling densities were greater in harvested plots than in heavily and moderately damaged areas. There were no differences between moderately (gaps) and heavily damaged stands in species diversity and seedling densities, increment growth and height. The amount of light reaching the ground should be considerably less in moderately damaged areas because of the remaining partial canopy, which should reduce the growth rates of regenerating seedlings (Harrington and Bluhm, 2001). One explanation of the apparent similarity between the two damage classes may be that the extremely large number of fallen trunks and coarse debris in heavily damaged areas provides shade (Ilisson *et al*., 2005). If this is so, a faster growth rate is to be expected in heavily damaged areas when regeneration exceeds the height of the fallen trunks.

Crushed vegetation and eliminated moss carpet due to windthrow can efficiently contribute to the establishment of seeds. As pits are the areas in the forest floor where mineral soil is exposed, they provide good opportunities for the germination and establishment of small-seeded species like birch and alder in our study, where spruce (intermediate-sized seeds) and rowan (large-seeded) showed indifference to microsite.

However, the environmental conditions of pits are quite unfavourable for seedlings. During spring or after a large precipitation event, seedlings in pits can suffer because of overflow (Harrington and Bluhm, 2001). At the same time, the temperatures increase near the soil surface. Thus pits can have very wet or very dry phases, depending on the weather conditions, a possible reason for the low density of some species in pits.

Survival of seedlings in tree-fall pits can be also problematic because of greater accumulation of litter and burial under soil slides falling from mounds during heavy rains (Ulanova, 2000; Harrington and Bluhm, 2001). The success of seedlings that germinate in pits may depend on individual growth rate, since taller trees may survive partial burial. Moreover, the competition within and between tree species is significant.

Norway spruce is one of the few natural tree species in Northern Europe that is able to establish itself in shade and grow into overstory. Spruce density certainly increased with decreasing disturbance severity. Although in our study they were smallest and lowest in density in pits compared to other microsites where birch and alder showed no marked difference, spruce seedlings had the lowest mortality figure of all species in pits. A reason for small seedlings and low densities of spruce in pits could be the later time of establishment because of difficult environmental conditions rather than the lower light availability in pits (Clinton and Baker, 2000). While the light availability and temperature are highest on mounds (Clinton and Baker, 2000), the regeneration densities were lowest there.

Natural regeneration in uncleared areas is a long-term process (Hytteborn and Packham, 1987) and future seedling establishment may increase as fallen logs decompose sufficiently to become good seedbeds (Hytteborn and Packham, 1987; Hofgaard, 1993; Wohlgemuth *et al.*, 2002). Observations by Wohlgemuth *et al.* (2002) suggest that fallen logs provide recruitment opportunities for Picea abies seedlings about seven years after the storm. Because only 3–4 years have passed since the storm events in our study areas, there was no regeneration found on logs – the fourth microsite in our study – as yet. Future research in these areas, with such a great amount of dead wood, should determine whether logs play an important role as seedbeds. In that case, we expect that the importance of spruce regeneration (according to literature spruce is the most common tree species to regenerate on logs) in uncleared areas will increase over several decades, producing a mixed, uneven-aged stand.

Two other functions of storm-felled trees are to protect seedlings against animal browsing (de Chantal and Granström, 2007) and possibly to alter nutrient dynamics. Some of the nutrients from the dead wood leaches into the forest soil (Hyvönen *et al.*, 2000; Laiho and Prescott, 2004) and can be taken up by regenerating seedlings (Krankina *et al.*, 1999).

Because the decomposition rate is found to be negatively correlated with size of dead wood (Harmon *et al.*, 1986; Harmon and Sexton, 1996; Krankina *et al.*, 1999; Mackensen *et al.*, 2003), uncleared areas with abundant dead wood may offer nutrient input from leaching for a longer period. Although 3-4 years after disturbance there was no change in CWD nutrient content and also in soil nutrient content. A pulse of dead wood is acting as temporary nutrient storage, but it often takes several decades of decay before dead wood starts to act as a nutrient source (Krankina *et al.*, 1999; Laiho and Prescott, 2004).

7. CONCLUSIONS

The evidence found in this thesis allows for some general statements and suggestions for the management of windthrow areas. At the wider scale (landscape level), windthrow gaps supply a continuity of different stages of decaying wood and different vegetation stages. At smaller scale (forest or stand level) these gaps increase species diversity.

Because of their contribution to regional biological diversity, some windthrow areas should not be managed (specially in protected areas), but retained as heterogeneous habitat islands and dead wood hotspots. Windthrow areas exhibit a wide range of CWD types, wider than the small-dimension slash left by today's cuttings.

Generally, when a forest with certain stand characteristics gets hit by a storm, part of the stands are entirely windthrown, some of them partly and some not get any damages. The division between these categories depends on storm characteristics. The remaining trees either 1) continue as living healthy trees, 2) are damaged but recover, 3) die and fall down later on either because they were initially damaged at the storm event or because they suffer from post-storm effects (**II**). The dead wood can be standing or lying, which influences decomposition to a high degree: laying dead wood decays considerably faster than leaning or standing dead wood, and the decomposition processes in open areas (totally damaged areas) were faster than under closed canopy (**III**). The amount of dead wood is higher in natural forests than in managed forests (**I**). The release of nutrients, and the period during which this happens, might be important for regeneration. Only a few years after the storm these effects have not been detected yet (**V**), but the uncleared storm damaged areas contribute to heterogeneity of the forest stand and hence to an increase of biodiversity (**IV**).

REFERENCES

Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in nortwestern Europe. Ann. Bot. Fennici 5, 169-211.

Andersson, L.I., Hytteborn, H., 1991. Bryophytes and Decaying Wood: A Comparison between Managed and Natural Forest. Holarct. Ecol. 14, 121-130.

Angelstam, P.K., 1996. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. In, IAVS Workshop on Disturbance Dynamics in Boreal Forests, Rouyn-Noranda, Canada, pp. 593-602.

Bobiec, A., 2002. Living stands and dead wood in the Bialowieza forest: suggestions for restoration management. Forest Ecology and Management 165, 125-140.

Boddy, L., 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecol. Bull. 49, 43-56.

Bouget, C., Duelli, P., 2004. The effects of windthrow on forest insect communities: a literature review. Biological Conservation 118, 281-299.

Brassard, B.W., Chen, H.Y.H., 2006. Stand Structural Dynamics of North American Boreal Forests. Critical Reviews in Plant Sciences 25, 115-137.

Brassard, B.W., Chen, H.Y.H., 2008. Effects of Forest Type and Disturbance on Diversity of Coarse Woody Debris in Boreal Forest. Ecosystems 11, 1078-1090.

Caylor, J., Pierce, J., Salazar, W., 1982. Optical bar panoramic photography for planning timber salvage in drought-stressed forests. Photogrammetric Engineering and Remote Sensing 48(5), 749-753.

Ciesla, W.M., Allison, R.A., Weber, F.P., 1982. Panoramic aerial-photography in forest pest-management. Photogrammetric Engineering and Remote Sensing 48(5), 719-723.

Clinton, B.D., Baker, C.R., 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. Forest ecology and management 126, 51-60.

Dahdouh-Guebas, F., Koedam, N., 2008. Long-term retrospection on mangrove development using transdisciplinary approaches: A review. Aquatic Botany 89, 80-92.

de Chantal, M., Granström, A., 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. Forest Ecology and Management 250, 3-8.
de Chantal, M., Leinonen, K., Kuuluvainen, T., Cescatti, A., 2003. Early response of *Pinus sylvestris* and *Picea abies* seedlings to an experimental canopy gap in a boreal spruce forest. Forest Ecology and Management 176, 321-336.
DeMars, C.J., Slaughter, G.W., Bedard, W.D., Norick, N.X., Roettgering, B., 1980. Estimating western pine beetle-caused tree mortality for evaluating an attractive pheromone treatment. Journal of Chemical Ecology 6(5), 853-866.
Dillman, R.D., White, W.B., 1982. Estimating mountain pine beetle-killed ponderosa pine over the front range of Colorado with high-altitude panoramic photography. Photogrammetric Engineering and Remote Sensing 48(5), 741-747.
Drobyshev, I.V., 2001. Effect of natural disturbances on the abundance of Norway spruce (*Picea abies* (L.) Karst.) regeneration in nemoral forests of the southern boreal zone. Forest Ecology and Management 140, 151-161.
Dyer, J.M., Baird, P.R., 1997. Wind disturbance in remnant forest stands along the prairie-forest ecotone, Minnesota, USA. Plant Ecology 129, 121-134.
Eriksson, M., Neuvonen, S., Roininen, H., 2007. Retention of wind-felled trees and the risk of consequential tree mortality by the European spruce bark beetle *Ips typographus* in Finland. Scand. J. For. Res. 22(6), 516-523.
Eriksson, M., Pouttu, A., Roininen, H., 2005. The influence of windthrow area and timber characteristics on colonization of wind-felled spruces by *Ips typographus* (L.). Forest Ecology and Management 216, 105-116.
FAO, ISSS, ISRIC, 1998. World reference base for soil resources. World Soil Resources Rep. 84. In, Rome.
Frelich, L.E., 2002. Forest Dynamics and Disturbance Regimes – Studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge.
Gromtsev, A., 2002. Natural Disturbance Dynamics in Boreal Forests of European Russian: a Review. Silva Fenn. 36(1), 41-55.

Göthlin, E., Schroeder, L.M., Lindelöw, A., 2000. Attacks by *Ips typographus* and *Pityogenes chalcographus* on windthrown spruces (*Picea abies*) during the two years following a storm felling. Scand. J. For. Res. 15(5), 542-549.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., K. Cromack, J., Cummins, K.W., 1986. Ecology of Coarse Woody Debris in Temperate Ecosystems. Adv. Ecol. Res. 15, 133-302.

Harmon, M.E., Krankina, O.N., Sexton, J., 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Can. J. For. Res. 30, 76-84.

Harmon, M.E., Sexton, J., 1996. Guidelines for measrements of woody detritus in forest ecosystems. U. S. LTER Publication No. 20.

Harrington, T.B., Bluhm, A.A., 2001. Tree regeneration responses to microsite characteristics following a severe tornado in the Georgia Piedmont, USA. Forest Ecology and Management 140, 265-275.

Hedgren, P.O., Schroeder, L.M., Weslien, J., 2003. Tree killing by *Ips typographus* (Cleoptera: Scolytidae) at stand edges with and without colonized felled spruce trees. Agricultural and Forest Entomology 5(1), 67-74.

Hofgaard, A., 1993. Structure and regeneration patterns in a virgin *Picea abies* forests in northern Sweden. Journal of Vegetation Science 4, 601-608.

Hytteborn, H., Packham, J.R., 1987. Decay rate of *Picea abies* logs and the storm gap theory: a re-examination of Sernander plot III, Fiby Urskog, central Sweden. Arbocult. J. 11, 299-311.

Hyvönen, R., Olsson, B.A., Lundkvist, H., Staaf, H., 2000. Decomposition and nutrient release from *Picea abies* (L.) Karst. and *Pinus sylvesteris* L. logging residues. Forest Ecology and Management 126, 97-112.

Ilic, J., Boland, D., McDonald, M., Downes, G., Blakemore, P., 2000. Woody density phase 1 - state of knowledge. In, National Carbon Accounting System Technikal Report No. 18. Australian Greenhouse Office, Canberra.

Ilisson, T., Metslaid, M., Vodde, F., Jõgiste, K., Kurm, M., 2005. Storm disturbance in forest ecosystems in Estonia. Scand. J. For. Res. 20 (Suppl. 6), 88-93.

Jonsson, B.G., 2000. Availability of Coarse Woody Debris in a Boreal Old-Growth *Picea abies* Forests Journal of Vegetation Science 11, 51-56.

Jonsson, B.G., Kruys, N., 2001. Ecology of coarse woody debris in boreal forests: future research directions. Ecol. Bull. 49, 279-281.

Karjalainen, L., Kuuluvainen, T., 2002. Amount and diversity of coarse woody debris within a boreal forest landscape dominated by *Pinus sylvestris* in Vienasalo wilderness, eastern Fennoscandia. Silva Fenn. 36, 147-167.

Kasesalu, H., 2001. Changes in the Nature Reserve District stands at Järvselja during the last six decades. Forestry studies XXXV, 74-88. (In Estonian with English abstract).

Klein, W.H., 1982. Estimating bark beetle-killed lodgepole pine with high-altitude panoramic photography. Photogrammetric Engineering and Remote Sensing 48(5), 733-737.

Krankina, O.N., Harmon, M.E., 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water, Air and Soil Pollution 82, 227-238.

Krankina, O.N., Harmon, M.E., Griazkin, A.V., 1999. Nutrient stores and dynamics of woody detritus in boreal forest: modeling potential implications at the stand level. Can. J. For. Res. 29, 20-32.

Krankina, O.N., Harmon, M.E., Kukuev, Y.A., Treyfeld, R.F., Kashpor, N.N., Skudin, V.M., Protatsov, N.A., Yatskov, M., Spycher, G., Povarov, E.D., 2002. Coarse woody debris in forest regions of Russia. Can. J. For. Res. 32, 768-778.

Krankina, O.N., Treyfeld, R.F., Harmon, M.E., Spycher, G., Povarov, E.D., 2001. Coarse woody debris in the forests of St. Petersburg region, Russia. Ecol. Bull. 49, 93-104.

Krigul, T., 1971. Metsataksaatori teadmik (Guidelines for forest taxation). Eesti põllumajanduse Akadeemia, Tartu (In Estonian).

Kuuluvainen, T., 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Annales Zoologici Fennici 31, 35-51.

Kuuluvainen, T., 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fenn. 36, 97-125.

Kuuluvainen, T., Juntunen, P., 1998. Seedling Establishment in Relation to Microhabitat Variation in a Windthrow Gap in a Boreal Pinus sylvestris Forest. Journal of Vegetation Science 9, 551-562.

Kuuluvainen, T., Syrjanen, K., Kalliola, R., 1998. Structure of a pristine *Picea abies* forest in northeastern Europe. Journal of Vegetation Science 9, 563-574.

Köster, K., Seedre, M., Jõgiste, K., Tukia, H., 2003. The quantitativemeasurements of coarse woody debris in Lahemaa and Karula National Parks in Estonia. Transactions of the Faculty of Forestry, Estonian Agricultural University 36, 55-70.

Laiho, R., Prescott, C.E., 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can. J. For. Res. 34, 763-777.

Lindemann, J.D., Baker, W.L., 2001. Attributes of blowdown patches from a severe wind event in the Southern Rocky Mountains, USA. Landscape Ecology 16, 313-325.

Linder, P., Elfving, B., Zackrisson, O., 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. Forest Ecology and Management 98, 17-33.

Lundqvist, L., Nilson, K., 2007. Regeneration dynamics in an uneven-aged virgin Norway spruce forest in northern Sweden. Scand. J. For. Res. 22, 304-309.

Lõhmus, E., 1984. Eesti metsakasvukohatüübid (Estonian forest site types) ENSV ATK IJV, Tallinn (In Estonian).

Lõhmus, P., Lõhmus, A., 2001. Snags, and their lichen flora in old Estonian peatland forests. Ann. Bot. Fennici 38, 265-280.

Lässig, R., Mocalov, S.A., 2000. Frequency and characteristics of severe storms in the Urals and their influence on the development, structure and management of the boreal forests. Forest Ecology and Management 135, 179-194.

Mackensen, J., Bauhus, J., Webber, E., 2003. Decomposition rates of coarse woody debris - A review with particular emphasis on Australian tree species. Australian Journal of Botany 51, 27-37.

Meier, F., Gall, R., Forster, B., 2003. Ursachen und Verlauf der Buchdrucker-Epidemien (*Ips typographus* L.) in der Schweiz von 1984 bis 1999. Schweizerische Zeitschrift für Forstwesen 154(11), 437-441.

Moseley, R.K., 2006. Historical landscape change in northwestern Yunnan, China - Using repeat photography to assess the perceptions and realities of biodiversity loss. Mountain Research and Development 26, 214-219.

Naesset, E., 1999. Decomposition rate constants of *Picea abies* logs in southeastern Norway. Can. J. For. Res. 29, 372-381.

Nageleisen, L.-M., 2001. Monitoring of bark and wood-boring beetles in France after the December 1999 storms. Integrated Pest Management Reviews 6, 159-162.

Okland, B., Berryman, A., 2004. Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. Agricultural and Forest Entomology 6(2), 141-146.

Peltonen, M., 1999. Windthrows and dead-standing trees as bark beetle breeding material at forest-clearcut edge. Scand. J. For. Res. 14(6), 505-511.

Peterson, C.J., Pickett, S.T.A., 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. Journal of Vegetation Science 1, 657-662.

Peterson, C.J., Pickett, S.T.A., 2000. Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. Oikos 90, 489-500.

Reintam, L., Rooma, I., Kull, A., 2001. Map of soil vulnerability and degradation in Estonia. In: Stott, D.E., Mohtar, R.H., Steinhard, G.C. (Ed.), Sustaining the Global Farm. 10th International Soil Conservation Organization Meeting. USDA-ARS NSERL, May 24-29, 1999, Purdue University, pp. 1068-1074.

Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. Canadian Journal of Botany-Revue Canadienne De Botanique 82, 1273-1283.

Rouvinen, S., Kuuluvainen, T., Karjalainen, L., 2002a. Coarse woody debris in old *Pinus sylvestris* dominated forests along a geographic and human impact gradient in boreal Fennoscandia. Can. J. For. Res. 32, 2184-2200.

Rouvinen, S., Kuuluvainen, T., Siitonen, J., 2002b. Tree Mortality in a *Pinus sylvesteris* Dominated Boreal Forest Landscape in Vienasalo Wilderness, Eastern Fennoscandia. Silva Fenn. 36(1), 127-145.

Ruel, J.C., Pineau, M., 2002. Windthrow as an important process for white spruce regeneration. Forestry Chronicle 78, 732-738.

Runkle, J.R., 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A., White, P.S. (Eds.), The ecology of natural disturbances and patch dynamics. Academic Press, Inc., Orlando, FL. 472p.

Samalens, J.C., Rossi, J.P., Guyon, D., Van Halder, I., Menassieu, P., Piou, D., Jactel, H., 2007. Adaptive roadside sampling for bark beetle damage assessment. Forest Ecology and Management 253, 177-187.

Samuelsson, J., Gustafsson, L., Ingelög, T., 1994. Dying and Dead Trees - a review of their importance for biodiversity. In. Swedish Environmental Protection Agency, Uppsala, p. 109.

Schroeder, L.M., 2001. Tree mortality by the bark beetle *Ips typographus* (L.) in storm-disturbed stands. Integrated Pest Management Reviews 6, 169-175.

Shorohova, E.V., Shorohov, A.A., 2001. Coarse woody debris dynamics and stores in a boreal virgin spruce forest. Ecol. Bull. 49, 129-135.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forest as an example. Ecol. Bull. 49, 11-41.

Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management 128, 211-225.

Sippola, A.L., Siitonen, J., Kallio, R., 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. Scand. J. For. Res. 13, 204-214.

Small, C.J., McCarthy, B.C., 2002. Effects of simulated post-harvest light availability and soil compaction on deciduous forest herbs. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 32, 1753-1762.

Stanturf, J.A., Goodrick, S.L., Outcalt, K.W., 2007. Disturbance and coastal forests: A strategic approach to forest management in hurricane impact zones. Forest Ecology and Management 250, 119-135.

Storaunet, K.O., 2004. Models to Predict Time Since Death of *Picea abies* Snags. Scand. J. For. Res. 19(3), 250-260.

Storaunet, K.O., Rolstad, J., 2002. Time since death and fall of Norway spruce lgs in old-growth and selectively cut boreal forest. Can. J. For. Res. 32(10), 1801-1812.

Storaunet, K.O., Rolstad, J., 2004. How long do Norway spruce snags stand? Evaluating four estimation methods. Can. J. For. Res. 34(2), 376-383.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., Roberts, D.W., 1997. Course woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecological Applications 7, 702-712.

Ulanova, N.G., 1998. The effects of windthrow on forests at different spatial scales: a review. In, Conference on Wind and Other Abiotic Risks to Forests, Jownsuu, Finland, pp. 155-167.

Ulanova, N.G., 2000. The effects of windthrow on forests at different spatial scales: a review. Forest Ecology and Management 135, 155-167.

Wichmann, L., Ravn, H.P., 2001. The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. Forest Ecology and Management 148, 31-39.

Wohlgemuth, T., Kull, P., Wüthrich, H., 2002. Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivian 1990. For. Snow Landsc. Res. 77, 17-47.

Voolma, K., 1998. A review of the history of forest entomology in Estonia. Teaduse ajaloo lehekülgi Eestist 12, 140-158. (In Estonian with English summary).

Voolma, K., 2002. Health condition of Estonian forests in the 1920-1930s. Proceedings of the Estonian Academic Forest Society 17, 61-71 (In Estonian with English summary).

Voolma, K., Õunap, H., Süda, I., 2000. Scolytidae. Distribution maps of Estonian insects, 2. Eesti Loodusfoto, Tartu.

Yatskov, M., Harmon, M.E., Krankina, O.N., 2003. A chronosequence of wood decomposition in the boreal forest of Russia. Can. J. For. Res. 33, 1211-1226.

SUMMARY IN ESTONIAN

Elusa ja surnud puidu biomassi dünaamika tormijärgses metsa ökosüsteemis.

Tugevad tuuled mõjutavad oluliselt meie metsade dünaamikat. Tormikahjustuste osakaal on aastate lõikes üha enam tõusnud, seega on antud teema muutunud aktuaalseks ja vajadus süvendatud uuringute järele kasvab, eriti pidades silmas kliimamuutuste võimalikku kasvavat mõju. Häiringujärgselt tekkiv lagunev, surnud puit, on tähtis komponent metsaökosüsteemides, olles tihedalt seotud loodusliku mitmekesisuse ja erinevate ökosüsteemisiseste protsessidega. Lagunev puit ökosüsteemis kujutab endast pikaajalist orgaanilise aine ja toiteainete ressurssi, elukohta mitmetele organismidele ja lõpuks on see väga oluline komponent metsamuldade koostises.

Majanduslikult on vajalik langetada otsused, milliseid metsanduslikke võtteid kasutada kahjustatud aladel vahetult peale tormikahjustust. Antud otsustest sõltub edaspidine majandusskeem ja kogu uue metsapõlvkonna areng. Majandustegevuse planeerimisel tuleb lähtuda mitte ainult vahetust kahjustusejärgsest olukorrast vaid ka pikemast arenguperspektiivist ning nii tormi kui teiste häiringute kordumise võimalusest.

Tormimurru koristamine ja uue metsapõlve istutamine on olnud pikaajaline praktika, mis suurel määral võimaldab tulundusmetsadest saadava puidukoguse maksimeerimist. Pidades silmas teisi eesmärke, eriti metsade looduslikkuse mitmekesisuse suurendamist väärivad igakülgset uurimist ka alternatiivsed majandusvõtted.

Käesoleva töö aluseks on unikaalne uurimisandmestik tormikahjustatud metsa püsikatsealadelt. Variantidena vaadeldakse erinevate metsanduslike meetoditega majandatud alasid, kaasa arvatud olukorda, kus tormimurdu ei koristata. Töö annab ülevaate tormialadel häiringujärgselt elus ja surnud puidu biomassi dünaamikas aset leidvatest muutustest. Töö koosneb viiest originaaluuringust (**I-V**).

Erineva intensiivsusega häiringud põhjustavad puistus erinevaid muutusi. Tugevad tormid võivad hävitada kogu puistu, samas nõrgemad tuuled võivad põhjustada ainult mõne üksiku puu surma. Esmase häiringu üle elanud puude saatus võib olla väga erinev. Nad kas: 1) jätkavad kui elujõulised ja terved puud; 2) on saanud kahjustada, kuid taastuvad; 3) Surevad ja mõne aja möödudes langevad maapinnale, kuna nad said niivõrd tõsiselt kahjustada esmase häiringu poolt, või põhjustab nende suremise esmasele häiringule järgnev häiring (tormikahjustusele järgneb kindlasti üraskikahjustus) (**II**).

Hukkunud puistu puitmaterjal jagatakse tavaliselt kaheks osaks: seisvad surnud puud/tüükad ja lamav/toetuv puitmaterjal, mis omakorda mõjutab oluliselt seda kuidas ja kui kiiresti leiavad lagunemiseprotsessid puidus aset. Lamav (maapinnale lähemal või kontaktis olev) puitmaterjal laguneb oluliselt kiiremini kui toetuv või seisev materjal. Täiestikahjustatud alal (kõik puud hukkunud häiringu tõttu) olev materjal laguneb kiiremini kui osaliselt kahjustatud alal (pooled puud puistus kahjustatud/hukkunud) olev puitmaterjal (**III**).

Kui võrdleme majandatud metsa ja loodusliku metsas (majandustegevust pole toimunud juba aastakümneid) ilmneb, et lagupuidu kogused majandatavas metsas on oluliselt madalamad kui looduslikus metsas (**I**), seda eelkõige seetõttu, et majandatavas metsas eemaldatakse jämedamõõtmeline materjal majandustegevuse käigus.

Lagunevat, surnud puitu, ja sinna kogunenud toiteainete aeglast vabanemist loetakse üheks väga oluliseks stabiliseerivaks faktoriks häiringujärgselt. Toiteainete säilitamine ja pikaajaline vabanemine lagupuidust on väga oluline uue puistu tekkele (uuendusele). Käesolevaks ajaks, kus häiringust on möödunud veidi üle viie aasta, ei ole toiteainete sisaldus lagupuidus veel oluliselt muutunud (**V**) ja lagupuidus olevad toiteained pole uuendust ja selle kasvu mõjutanud.

Uuenduse seisukohalt uuenevad kõige paremini tormijärgselt koristatud alad, kus puitmaterjali ülestöötamisega paljastati mineraalmaad väga suures ulatuses ja kus pioneerpuuliigid said kiirelt kasvama hakata. Osaliselt- ja täiestikahjustatud alad uuenevad tunduvalt aeglasemalt, kuid sealne puistustruktuuri ebaühtlane areng loob metsaökosüsteemi, mis tänu oma erivanuselisusele ja liigirikkusele on uutele häiringutele vastupidavam (**IV**).

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I

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ORIGINAL ARTICLE

Variation and ecological characteristics of coarse woody debris in Lahemaa and Karula National Parks, Estonia

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Abstract

The coarse woody debris (CWD) was inventoried in two boreal Estonian conifer-dominated forest landscapes/national parks, Lahemaa and Karula, with different forestry history and management intensity. The inventoried areas in both national parks consisted of a core with a strict nature reserve (unmanaged) and the surrounding protected special and restricted management zones (management activities in the past). Stands with no records of silvicultural activity since the 1920s (unmanaged) were compared with traditionally harvested stands. CWD was measured as standing dead trees, logs and snags >10 cm in diameter and >1.3 m in length in 304 circular plots (Lahemaa 134 plots, Karula 170 plots; $r=11.28$ m, 400 m^2). The volumes of CWD varied considerably between individual stands. The mean volume of CWD (standing and down combined) in Lahemaa was 48.5 m^3 ha^{-1}, ranging from 0.6 to 148.6 m^3 ha^{-1}. The mean volume of CWD in Karula was 27.6 m^3 ha^{-1}, ranging from 0.2 to 193.7 m^3 ha^{-1} from stand to stand. On average, 19.5 m^3 ha^{-1} (40.2%) of CWD in Lahemaa was standing dead wood and 29.1 m^3 ha^{-1} (59.8%) down dead wood. In Karula standing dead wood formed 15.2 m^3 ha^{-1} (55.7%) and down dead wood 12.2 m^3 ha^{-1} (44.3%). Variation in CWD volumes was clearly dependent on the management history of the stands. Stands with a documented history of management (e.g. cuttings and thinnings) had significantly lower CWD volume than natural stands found mainly in strict nature reserves. Stands selectively logged a long time ago (more than approximately 60 years) did not differ considerably from natural stands in the amount of CWD. The amount of CWD in managed stands (Lahemaa 14.1 m^3 ha^{-1} and Karula 10.6 m^3 ha^{-1}) was comparable to other studies in silviculturally managed forests in the boreal zone. The study shows that CWD amounts in Estonian conditions are similar to previous studies in this region.

Keywords: *Boreal forest, coarse woody debris, management history, natural and selectively managed stands, nature conservation.*

Introduction

Dead wood is recognized as an important component of forest ecosystems linked to biodiversity and ecosystem processes (Esseen et al., 1992; Samuelsson et al., 1994; Angelstam, 1998; Arsenault, 2002; Karjalainen & Kuuluvainen, 2002). The crucial role of dead and dying wood for the biodiversity (e.g. invertebrates, swamps and lichens) of boreal and boreo-nemoral forests has been emphasized by several authors (Haila et al., 1993; Samuelsson et al., 1994; Niemelä, 1997; Angelstam, 1998; Linder & Östlund, 1998; Kuuluvainen et al., 2005).

There is a general lack of knowledge of dead wood dynamics in forest ecosystems. Although the microbiological aspects have been covered in the literature (Harmon et al., 1986), specific models are needed to combine the effects of key groups in boreal forests (e.g. decaying swamps, saproxylic species, woodpeckers) and their effects on a certain stage and habitat type of forests, predicting the amount of dead wood and succession.

Dead wood, also known as coarse woody debris (CWD), is commonly treated as two fractions in

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studies: standing dead trees and down woody material (according to Bobiec, 2002).

The amount of dead wood in a natural forest depends basically on three factors: the fertility of the site, the decaying process of dead trees (position, species, microclimate, fungal decomposition) and disturbances that affect the mortality rates and patterns of trees (Harmon et al., 1986; Jonsson, 2000; Siitonen, 2001; Tonteri & Siitonen, 2001). The formation of dead wood is largely driven by natural disturbance agents, such as storms and wildfires (Harmon et al., 1986; Esseen et al., 1992; Samuelsson et al., 1994; Kuuluvainen et al., 2005). In natural conditions, recurring disturbances, either small-scale gap perturbations or large-scale stand-replacing catastrophic events (continuously but irregularly) replenish and create CWD (Kuuluvainen, 1994; Siitonen et al., 2000; Kuuluvainen et al., 2005). The ultimate effect of a disturbance (tornado-like strong turbulent winds) can kill and fell all the trees in a large area instantly.

In natural south and middle boreal forests in Fennoscandia, the amount of dead wood is reported to be between 60 and 120 m^3 ha^{-1} (Linder et al., 1997; Jonsson, 2000; Siitonen, 2001; Sippola, 2001; Karjalainen & Kuuluvainen, 2002). In general, pine-dominated forests have lower CWD volumes than spruce-dominated ones (Sippola, 2001; Tonteri & Siitonen, 2001). Most studies have found that about 30% of the total CWD volume is in standing dead trees and 70% in down woody material and stumps. In pine-dominated forests the standing part of the total CWD volume is usually higher than in spruce-dominated ones (Tonteri & Siitonen, 2001).

In Fennoscandia, intensive forest management has considerably reduced the amount of decaying wood (Linder & Östlund, 1992; Siitonen et al., 2000). The regular thinning of stands, clear-cut harvesting, efficient forest fire prevention, etc., have all contributed to a general decrease in CWD in managed forests (Siitonen et al., 2000). There are also forests where no silviculture has been practised during the past few decades, but which bear signs of impact in earlier days. These kinds of forests have been called, among other things, selectively logged (Rouvinen, 2002). Selectively logged/semi-natural stands have still a quite high volume of CWD compared with managed stands and almost the same volume of CWD as natural stands, but they can be poorer in decaying wood-associated (saproxylic) species than natural stands (Rouvinen, 2002). The diversity of species, including autotrophs and heterotrophs, depending on dead wood is higher in unmanaged forests (Andersson & Hytteborn, 1991). In addition, the presence of different decay classes typical for old-growth forests enhances the biological diversity (Renvall, 1995). Wood of large-diameter classes (>20 cm) is particularly important for threatened and rare saproxylic species (Andersson & Hytteborn, 1991; Jonsell et al., 1998; Siitonen, 2001; Rouvinen, 2002). One reason for this may be that large trunks decay more slowly than twigs, branches and small trunks (Harmon et al., 1986; Sippola, 2001). By holding more moisture, they provide continuous and more stable substrate suitable for specialist species. Large-diameter trunks are suitable habitats for a greater number of organisms and cannot easily be replaced (Arsenault, 2002).

The main aim of the present study was the description of CWD (status) in formerly managed and untouched (minimum 60 years without interference in the course of the last century) stands in two hemiboreal Estonian National Park forest ecosystems. It was hypothesized that the amount of CWD is higher in unmanaged areas and that management history predicts the amount of CWD.

Materials and methods

Study areas

The study areas are situated in north-east Estonia in Lahemaa National Park (59°31′ N 25°90′ E) and in south-east Estonia in Karula National Park (57°43′ N 26°35′ E) in the hemiboreal vegetation zone (Ahti et al., 1968) (Figure 1).

A national park may belong to one of the following protection categories: strict nature reserve, special management zone or restricted management zone. Usually these three categories are combined over the whole area, to ensure the most effective protection of biodiversity.

In Lahemaa and Karula National Parks two areas were selected with different management histories (one strict reserve and one managed area). In total, 304 sample plots (134 in Lahemaa, 170 in Karula)

Figure 1. Map of the Baltic Sea region. Circle (a) marks Lahemaa National Park and circle (b) marks Karula National Park.

of 11.28 m radius were randomly located for the dead wood inventory. The area under study (different management histories) in Lahemaa was 141 ha and the total area of sample plots was 5.36 ha (3.8% of the total, regarding both strict nature reserve and managed areas). The area in Karula was 158.6 ha (different management histories) and the total area of sample plots was 6.8 ha (4.3% of the total, regarding both strict nature reserve and managed areas zones). The inventory took place in summer 2001.

Lahemaa National Park was established in 1971. The area of the national park is 725 km^2, of which 474 km^2 is land and 251 km^2 is sea. Sixty per cent of the forests in the park are owned by private citizens. As mentioned above, certain areas (belonging mainly to special and restricted management zone) of the national park are partly managed by traditional methods.

The forest flora of Lahemaa, as in the whole of north Estonia, is quite poor. More than 70% of Lahemaa's territory is covered with forests. The majority of them are dry boreal, heath and ombrotrophic bog forests, poor in species (Kalda, 1988). The Lahemaa study area is divided by the Baltic Ice Lake shore (esker and sand formations) into two different types of forest: pine-dominated forests growing on the sandy plateau of the Baltic Sea in the south, and moist and rich spruce-dominated mixed forests growing on the wet north-facing slopes. The main conifers in study area were Norway spruce [*Picea abies* (L.) Karst.] (38% from the stands) and Scots pine (*Pinus sylvestris* L.) (34% from the stands). Birch (*Betula pendula* Roth and *B. pubescens* Ehrh.) (20% from the stands) and black alder [*Alnus glutinosa* (L.) J. Gaertn.] (8% of the stands) were the most common deciduous trees. The average age of the studied stands was 80 years (range 40–200 years). Coniferous-dominated forests are considered to be mature after 90 years and deciduous-dominated areas after 75 years in Estonia.

The Karula National Park was created in 1993 and since 1979 it has been a landscape reserve (meaning that more intensive management is allowed). The smallest national park in Estonia, it covers 111 km^2 and was created to protect the typical south-east Estonian forest- and lake-rich landscapes. About 70% of the park area is covered with forests. The majority of the sampling plots were placed inside and close to strict nature reserve. The reserve has been outside commercial forestry for more than 30 years. The study also included the surrounding areas of reserve belonging to special and restricted management zones of the park. The main tree species in study area were Scots pine (75% of the stands), Norway spruce (14% of the stands) and birch (17% of the stands). The average age of the studied stands was 75 years (range 20–160 years).

Historical data

The average ages of the stands were taken from forestry inventory data. The detailed management history data (cutting type, time and intensity) were available only for Lahemaa, and the descriptions went back to the beginning of the 1920s (Juhandi, 1991). For Karula only records on management activity were available, without specification of concrete management operation. To have comparable data describing the influence of management history on CWD, all old stand records from both national parks were used. The analysis of more detailed management history was possible only for Lahemaa. The clear-cutting, selective cutting and thinned areas were compared with the unmanaged situation. Management history was based on old maps and inventory records. In the case of spruce and pine stands, all stands older than 90 years were used; in the case of birch and black alder, all stands older than 75 years were included.

Sampling and measurements

The sampling unit in managed and unmanaged areas was the tree stand. Inside each stand (uniform forest subcompartment with size >0.1 ha) sample plots were located at random. In stands with area <1 ha one plot was established, while in larger stands two or even three or four sample plots were established. Sample plots were circular, with 11.28 m radius (0.04 ha). In each plot all standing and lying dead wood with diameter >10 cm at the thinner end was measured. For standing dead trees (minimum height 1.3 m) the following variables were recorded: tree species, diameter at breast height, height of the tree/snag and decay stage, divided into five groups. For lying dead wood the following variables were recorded: tree species, diameter at both ends of stumps (thin and large end), decay stage divided into five classes (decay data were not analysed in this work) and the way of falling (natural/cut). In the case of stumps all stump diameters and decay stages were measured, but natural stumps were separated from artificial ones, where possible. The sampling system and the CWD measuring methods and classification used in the fieldwork are described more detailed in Jaakkola et al. (2005).

The Estonian forest management site index classification system according to Krigul (1971) was used to describe stand quality and productivity of the site (Table I). The site type, age, standing

Table I. Site index classification system according to Krigul (1971).

	Average height of trees (m) in stands with different site index				
Age (years)	I	II	III	IV	V
60	>20	19–17	16–14	13–11	<10
80	>24	23–21	20–17	16–14	<13
100	>27	26–24	23–20	19–16	<15

stock and management history data were taken from local forestry inventory databases.

Statistical analyses

Before data processing, the binary logarithm was calculated for the recorded CWD volume measurements to approximate the residual distribution of this variable to the normal distribution. Five observations with residuals higher than 3.5 were excluded as obvious measurement errors. After this filtering, the residual distribution of CWD appeared to be very similar to a normal distribution, the one that is assumed in analysis of variance (ANOVA).

The main statistical analysis was carried out with the SAS procedure Mixed (Release 8.2). This procedure realizes the general linear mixed model analysis (SAS Institute, 1999), which in the present case enables one to test whether, and how, the tree stand properties determine the CWD volume in the stand. The questions concerning the influence of various tree stand factors on CWD were formulated as specifically tailored Estimate and Contrast statements of the basic Mixed procedure. Results are presented in the form of two ANOVA tables.

The final version of the mixed model that was used to draw statistical conclusions consisted of four factors (see Appendix 1). The factors National park (two levels) and Forest type (six levels) were of classification type; the other factors, Stand age and Site index, were treated as continuous numerical factors (covariates). The two last factors were included in the model through cubic polynomials, whereas age dependence was presented by different polynomials for different national parks. The same model but with Site index replaced by Standing volume was used to obtain p-values for Standing volume. It was decided not to include these two factors simultaneously because the site index is highly correlated with the standing stock volume. Apart from the mixed model analysis described above, the simple one-way ANOVA was used to compare stands that had been managed in the past with unmanaged stands.

Results

Different management history influences the amount and diversity of CWD. ANOVA demonstrated that in areas where there has been no management the amount of CWD was significantly greater ($p = 0.0404$) than in areas where there have been occasional silvicultural operations (selective cuttings).

In the stands in Lahemaa with no management, the average amount of CWD was 85.9 m^3 ha^{-1} (range 28.3–148.6 m^3 ha^{-1}). In managed areas in Lahemaa, the average amount of CWD was 63.2 m^3 ha^{-1} (range 24.3–134.4 m^3 ha^{-1}; here, only mature forests are taken into consideration). In clear-cut areas the average amount of CWD was 51.2 m^3 ha^{-1} and in thinned areas it was 75.1 m^3 ha^{-1} (only mature forests are taken into consideration). When all stands were taken into consideration, the amount of CWD in managed stands was 14.1 m^3 ha^{-1} in Lahemaa and 10.6 m^3 ha^{-1} in Karula.

Although management has not been active in areas designated for national parks the differences in CWD are considerable. In Lahemaa the mean CWD volume was 48.5 m^3 ha^{-1}. Pine-dominated forests had a considerably lower CWD volume than spruce-dominated forests, 18.2 and 69.4 m^3 ha^{-1}, respectively (Table II). In Karula the mean CWD volume was 27.6 m^3 ha^{-1} and varied on average from 9.6 m^3 ha^{-1} in birch-dominated

Table II. Area and volumes ($\pm$SE) of total, standing and down coarse woody debris (CWD) in Lahemaa, by dominant tree species.

	Area (ha)	Total CWD (m^3 ha^{-1})	Standing CWD (m^3 ha^{-1})	Fallen CWD (m^3 ha^{-1})
All plots ($n = 79$)	141	48.46±2.41	19.49±1.13	29.07±1.61
Norway spruce ($n = 30$)	68.4	69.4±4.06	25.49±2.04	43.82±2.79
Birch sp. ($n = 16$)	23.7	52.87±4.93	23.52±2.4	30.01±3.45
Scots pine ($n = 27$)	38.4	18.2±2.09	9.46±1.09	8.72±1.2
Black alder ($n = 6$)	10.5	68.19±8.97	23.86±5.82	44.35±4.44

Table III. Area and volumes ($\pm$SE) of total, standing and down coarse woody debris (CWD) in Karula, by dominant tree species.

	Area (ha)	Total CWD (m^3 ha^{-1})	Standing CWD (m^3 ha^{-1})	Fallen CWD (m^3 ha^{-1})
All plots ($n=109$)	158.6	27.59 ± 1.54	15.19 ± 0.88	12.23 ± 0.87
Norway spruce ($n=15$)	15.4	33.81 ± 4.67	15.66 ± 1.71	17.56 ± 3.43
Birch sp. ($n=19$)	22.4	9.61 ± 2.36	8.48 ± 2.37	1.06 ± 0.21
Scots pine ($n=75$)	120.8	30.95 ± 1.88	16.82 ± 1.07	14.02 ± 1.01

forests to 30.9 m^3 ha^{-1} in pine-dominated forests (Table III).

The CWD volume was significantly affected by standing stock volume, site index, site type and age (Table IV). Standing stock and site index are strongly correlated, so it was not reasonable include these two factors simultaneously in the model. In each national park different factors had the strongest influence on CWD volumes. In Lahemaa, the factors having the strongest influences on amount of CWD were stand age ($p=0.008$) and site index ($p=0.02$). In Karula, the most important factor affecting the amount of CWD was standing stock ($p=0.02$).

Volume of CWD depends on site index class. In Lahemaa, CWD formed 21% of the standing stock of the stands. It varied from 6% in site index class V (the lowest site index class) to 24% in site index classes I and II. In Karula the volume of CWD formed 15% of the total timber volume of the stand. It varied from 11% in site index class V to 19% in site index class I. No significant difference in CWD volume was found between Karula and Lahemaa (Table V).

The CWD volume increased significantly with stand age in the studied area (Table IV). The partition of the stands into age classes clearly revealed that with increasing age, both the amount of standing stock and CWD are increasing until a certain age (Figures 2 and 3). In mature stands, the volume of neither standing stock nor CWD changed with age.

The volume of CWD did not depend on either the site type (Lahemaa, $p=0.09$; Karula, $p=0.37$) or dominant tree species (Lahemaa, $p=0.65$; Karula, $p=0.07$). There were some tendencies, but these were not significant statistically. In Karula, where pine was the dominant species in CWD (76% of measured stands were pine dominant), standing CWD volume exceeded usually fallen CWD (Figure 4). In Lahemaa the opposite tendency was observed in first three site index classes owing to Norway spruce dominance. In site index classes IV and V, which were mostly dominated by pine, the volumes of standing CWD and fallen CWD were almost equal (Figure 5).

Discussion

The results of this study are consistent with other studies of CWD stores in similar managed and unmanaged ecosystems. For example, in southern Finland the CWD volume in mature and overmature silviculturally managed forests was 14.4 and 23.3 m^3 ha^{-1}, respectively (Siitonen, 2001; Tonteri & Siitonen, 2001). In the St Petersburg region of Russia, the volume of CWD in mature and overmature forests was 24 m^3 ha^{-1} (Krankina et al., 2002). In natural or semi-natural forests in the southern boreal forest zone the amount of CWD can be much higher, from 70 to 184 m^3 ha^{-1} depending on the successional stage of the stand and the input rate caused by disturbances (Siitonen et al., 2000). In virgin taiga forests in north-western Russia, the proportion of CWD can be as much as 35–40% of the total volume (Kuuluvainen et al., 1998). In northern Finland, in old-growth timberline forest, the CWD volumes corresponded to 20–30% of the total timber volume (living and

Table IV. Analysis of logarithmically transformed total coarse woody debris (CWD) (both areas together): ANOVA type 3 test results for factors and contrasts.

Factor or contrast	NDF	DDF	F	p-value
Stand age in Karula	3	165	103.17	<0.0001
Stand age in Lahemaa	3	165	38.71	<0.0001
Difference between the age dependencies in Karula and Lahemaa	3	165	1.19	0.3165
Site index	3	165	6.74	0.0003
Standing stock volume	3	165	11.0	<0.0001
Site type	6	165	2.81	0.0124
Dominant tree species	2	165	1.15	0.318

Note: NDF = numerator degrees of freedom for the F-test; DDF = denominator degrees of freedom; F = value of the F-statistic; p-value tests the null hypothesis "Factor or contrast has no effect on CWD volume".

Table V. Analysis of logarithmically transformed total coarse woody debris (CWD) (both areas together): comparisons of effects of site index factor levels.

Comparison	Estimate	SE	*t*	*p*
Karula–Lahemaa	2.590	1.604	1.61	0.1083
SI_I–SI_V	2.174	0.524	4.15	<0.0001
SI_I–SI_{IV}	1.590	0.397	4.01	<0.0001
SI_I–SI_{III}	1.063	0.310	3.42	0.0008
SI_I–SI_{II}	0.548	0.246	2.22	0.0276
SI_{II}–SI_V	1.626	0.498	3.26	0.0013
SI_{II}–SI_{IV}	1.042	0.381	2.74	0.0069
SI_{II}–SI_{III}	0.515	0.205	2.51	0.0130
SI_{III}–SI_V	1.110	0.468	2.37	0.0189
SI_{III}–SI_{IV}	0.527	0.204	2.58	0.0106
SII_{IV}–SI_V	0.583	0.393	1.48	0.1396

Note: SII, …, SIV = levels of the site index factor; Estimate = difference between logarithmic CWD values at compared factor levels; SE = standard error of the estimate; t = value of the t-statistic (165 degrees of freedom for denominator); p = p-value for the null hypothesis "Value of the comparison is zero".

dead) of the stand (Sippola, 2001). There seems to be a north–south gradient of rising CWD volume which is comparable to the total tree volume (and richness) of the site (Linder et al., 1997; Siitonen, 2001; Sippola, 2001). The higher the natural tree volume, the greater the amount of CWD in natural forests. The same tendency was observed in this study.

The dynamics and amount of CWD are different in natural and managed stands. The low CWD volumes (14.1 m^3 ha^{-1} in Lahemaa and 10.6 m^3 ha^{-1} in Karula) are typical for managed forests, because silvicultural thinning reduces mortality by self-thinning and the recruitment of dead trees (Rouvinen, 2002). According to the model by Siitonen et al. (2000) for natural stands, in the first 100 years trees are dying mostly during catastrophic disturbances (such as forest fire and wind damage). With harvesting, mostly with clear-cut harvesting, most of the large-diameter trunks are removed from forests. Some cutting practices cause an input of CWD, whereas some clearly destroy the CWD (Hautala et al., 2004). The amounts in managed stands are usually low compared with amounts produced by natural disturbances. In old stands the importance of mortality caused by senescence and small-scale gap disturbances increases with stand age. The short rotation periods in managed forest reduce this development before large-diameter dead trees start to accumulate. In unmanaged, natural old forests, the amount of CWD stays stable. However, in this study the range of variation in Lahemaa was great. The CWD volume varied in unmanaged stands from 28.3 to 148.6 m^3 ha^{-1}. The dynamics of dead wood can be described by input and output (the accumulating new CWD can be approximately the same as the amount of decaying wood), which contains a typical mass balance model (Shugart, 2003).

The results of this study reveal that the main factor affecting the amount of CWD in studied stands was the volume of living trees (standing stock), which is in accordance with earlier studies in northern Europe (Linder et al., 1997; Siitonen, 2000; Sippola, 2001; Köster et al., 2003). Standing volume is, in turn, highly influenced by site productivity (Sippola, 2001; Rouvinen, 2002) and the age of the stand (Siitonen, 2000; Krankina et al., 2001; Köster & Seedre, 2003).

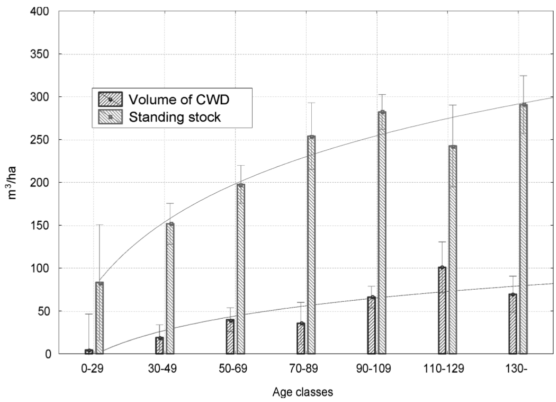

Figure 2. Volumes and inner spreads of total coarse woody debris (CWD) and standing stock by tree age classes in Lahemaa.

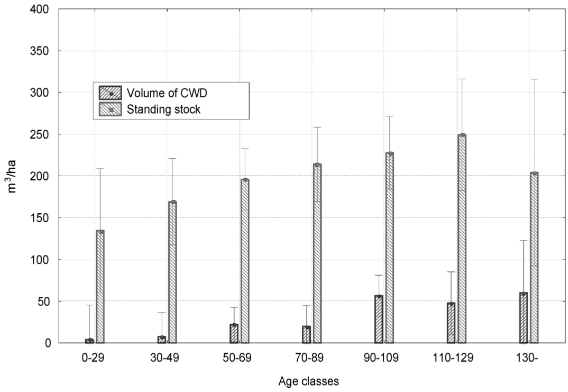

Figure 3. Volumes and inner spreads of total coarse woody debris (CWD) and standing stock by tree age classes in Karula.

In Lahemaa, there were large variations between stands when comparing standing stock and volume of CWD. A part of the study plots was inside quite recently fallen windthrow gaps of several hectares, so the high amount of CWD, not surprisingly, was making up for almost all of the original standing tree volume (hundreds of cubic metres). One reason why standing stock is important in Karula may be that the stands with high standing stock in many of the sampled areas were less than 1 ha in size. Small, randomly placed sample plots may not characterize the whole stand correctly (lower or higher amounts of CWD than they actually contain).

The results of this study revealed that in reserves (in unmanaged areas) there is a considerably higher amount of CWD than in protection zones (buffers around strict nature reserves that have been occasionally managed). Areas in Lahemaa, which had been clear-cut at the beginning of twentieth century, had a much lower volume of CWD than in areas that had been thinned. In areas that were not managed the amount of CWD was at the same level as in areas where there had been selective cuttings.

In the published CWD studies in Estonia, Kasesalu (2001) measured CWD in a small (19.3 ha) old protected area in Järvselja, east Estonia, and found that average CWD amounts were great: 98.99 ± 59.7 m^3 ha^{-1} [23% (9–40) of the total stand volume]. In Alam-Pedja National Park in Central Estonia, Lõhmus and Lõhmus

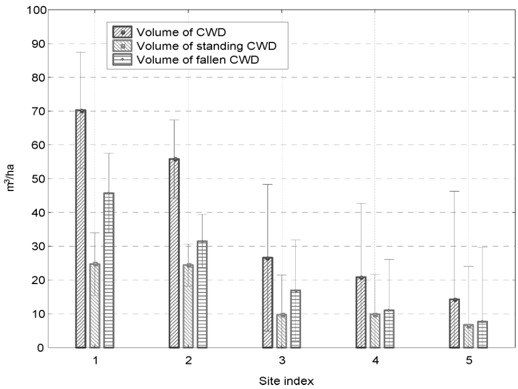

Figure 4. Volume and variation of coarse woody debris (CWD) and proportions of standing CWD and fallen CWD by site index classes in Lahemaa (site index classes are according to Krigul, 1971).

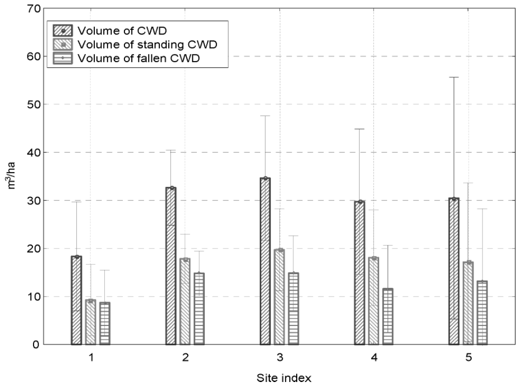

Figure 5. Volume and variation of coarse woody debris (CWD) and proportions of standing CWD and fallen CWD by site index classes in Karula (site index classes are according to Krigul, 1971).

(2001) found that amounts of standing CWD were 21 m^3 ha^{-1}. In the present study the volume of CWD was on average 48.5 m^3 ha^{-1} in Lahemaa and 27.6 m^3 ha^{-1} in Karula. The percentage of CWD from total timber volume was on average 21% in Lahemaa and 15% in Karula.

Clear stand effects can be seen in the CWD measurements, but others can be linked directly to the silvicultural methods used in the past, the lack of very decayed trees, almost total lack of CWD in certain areas and the homogeneous and steady-aged living tree cohorts. The parts with highest CWD volumes are comparable to the natural forests in the regional context.

Because the largest (in diameter) CWD is the most valuable local resource in the coniferous forests in the long run, the protected areas are extremely valuable as reference areas and core areas. Often because of the similar silvicultural background of protected areas all over Scandinavia and northern Europe, CWD is a critical resource limiting the existence (possibilities) of species and continuity of forest habitats. The long time-lag between tree death and its development to a relatively short time-scale log habitat makes it very difficult to restore parts of the "original" biodiversity and prevents endangered species by increasing the local extinction risk. A carefully planned and far-reaching restoration programme of those areas poorest in CWD is strongly recommended.

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References

Ahti, T., Hämet-Ahti, L. & Jalas., J. (1968). Vegetation zones and their sections in the north-western Europe. *Annales Botanici Fennici*, *5*, 169–211.

Andersson, L. I. & Hytteborn, H. (1991). Bryophytes and decaying wood—A comparison between managed and natural forests. *Holarctic Ecology*, *14*, 121–130.

Angelstam, P. K. (1998). Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science*, *9*, 593–602.

Arsenault, A. (2002). Managing coarse woody debris in British Columbia's forests: A cultural shift for professional forester? In W. F. Laudenslayer, P. J. Shea, B. E. Valentine, C. P. Weatherspoon & T. E. Lisle (Technical Coordinators), *Proceedings of the symposium on the ecology and management of dead wood in western forests*, Reno, NV, 2–4 November 1999 (Gen. Tech. Rep. PSW-GTR-181, pp. 869–878). Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Bobiec, A. (2002). Living stands and dead wood in the Bialowieza forest: Suggestions for restoration management. *Forest Ecology and Management*, *165*, 125–140.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1992). Boreal forests—The focal habitats of Fennoscandia. In L. Hansson (Ed.), *Ecological principles of nature conservation. Applications in temperate and boreal environments* (pp. 252–325). London: Elsevier Science.

Haila, Y., Hanski, I. K., Niemelä, J., Punttila, P., Raivio, S. & Tukia, H. (1994). Forestry and the boreal fauna: Matching management with natural forest dynamics. *Annales Zoologici Fennici*, *31*, 187–202.

Harmon, M. E., Franlin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., et al. (1986). Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, *15*, 133–320.

Hautala, H., Jalonen, J., Laaka-Lindberg, S. & Vanha-Majamaa, I. (2004). Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. *Biodiversity and Conservation*, *13*, 1541–1554.

Jaakkola, S., Tukia, H. & Lindholm, T. (2005). The quality of coarse woody debris (CWD) and aspects of naturality in two national parks in Estonia. *Suomen Ympäristö*, submitted. (In Finnish with English abstract.)

Jonsell, M., Weslien, J. & Ehnström, B. (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, *7*, 749–764.

Jonsson, B. G. (2000). Availability of coarse woody debris in an old-growth boreal spruce forest landscape. *Journal of Vegetation Science*, *11*, 51–56.

Juhandi, A. (1991). *Koljaku-Oandu reservaadi puistud ja nende seisund* (Koljaku-Oandu reserve: Stands and their description) (Trans. by authors). Eesti Graduation Thesis, Põllumajanduse Akadeemia, Tartu. (In Estonian.)

Kalda, A. (1988). Lahemaa rahvuspargi taimkatte ja selle geobotaanine liigestus (Plant cover and geobotanical division of Lahemaa National Park. In I. Etverk (Ed.), *Lahemaa uusimused III. Rahvuspargi looduse inventeerimine* (pp. 68–87). Tallinn: Valgus. (In Estonian with English abstract.)

Karjalainen, L. & Kuuluvainen, T. (2002). Amount and diversity of coarse woody debris within a boreal forest landscape dominated by *Pinus sylvestris* in Vienansalo wilderness, eastern Fennoscandia. *Silva Fennica*, *36*, 147–167.

Kasesalu, H. (2001). Changes in the Nature Reserve District stands at Järvselja during the last six decades. *Metsanduslikud Uurimused*, *XXXV*, 74–88. (In Estonian with English abstract.)

Köster, K. & Seedre, M. (2003). *Coarse woody debris analysis in Karula and Lahemaa National Parks*. Graduation Thesis, Estonian Agricultural University, Tartu. (In Estonian with English abstract.)

Köster, K., Seedre, M., Jõgiste, K. & Tukia, H. (2003). The quantitative measurements of coarse woody debris in Lahemaa and Karula National Parks in Estonia. In Postgraduate Research Papers at the Faculty of Forestry. *Transactions of the Faculty of Forestry. Estonian Agricultural University*, *36*, 55–70.

Krankina, O. N., Treyfeld, R. F., Harmon, M. E., Spycher, G. & Povarov, E. D. (2001). Coarse woody debris in the forest of the St. Petersburg region, Russia. *Ecological Bulletins*, *49*, 93–104.

Krankina, O. N., Harmon, M. E., Kukuev, Y. A., Treyfeld, R. F., Kashpor, N. N., Kresnov, V. G., et al. (2002). Coarse woody debris in forest regions of Russia. *Canadian Journal of Forest Research*, *32*, 768–778.

Krigul, T. (1971). *Metsataksaatori teadmik* (Guidelines for forest taxation). Tartu: *Eesti Põllumajandus Akadeemia*. (In Estonian.)

Kuuluvainen, T. (1994). Gap disturbance, ground microtopography, and the regeneration dynamics of the boreal coniferous forests in Finland: A review. *Annales Zoologici Fennici*, *31*, 35–51.

Kuuluvainen, T., Syrjänen, K. & Kalliola, R. (1998). Structure of pristine spruce taiga in north-eastern Europe. *Journal of Vegetation Science*, *9*, 563–574.

Kuuluvainen, T., Tukia, H. & Aapala, K. (2005). Ecological restoration of forested ecosystems in Finland. In J. A. Stanturf, & P. Madsen (Eds.), *Restoration of the boreal and temperate forests* (pp. 285–298). Boca Raton, FL: CRC Press.

Linder, P. & Östlund, L. (1992). Changes in the boreal forests of Sweden 1870–1991. *Svensk botanisk tidskrift*, *86*, 199–215. (In Swedish with English summary.)

Linder, P. & Östlund, L. (1998). Structural changes in three midporeal Swedish forest landscapes, 1885–1996. *Biological Conservation*, *85*, 9–19.

Linder, P., Elfving, B. & Zackrisson, O. (1997). Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management*, *98*, 17–33.

Lõhmus, P. & Lõhmus, A. (2001). Snags, and their lichens in old Estonian peatland forests. *Annales Botanici Fennici*, *38*, 265–280.

Niemelä, J. (1997). Invertebrates and the boreal forest management. *Conservation Biology*, *11*, 601–610.

Renvall, P. (1995). Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia*, *35*, 1–51.

Rouvinen, S. (2002). *Amount, diversity and spatio-temporal availability of dead wood in old forest in boreal Fennoscandia* (Research Notes 140). Faculty of Forestry, University of Joensuu.

Samuelsson, J., Gustafsson, L. & Ingelög, T. (1994). *Dying and dead trees—A review of their importance for biodiversity*. Uppsala: Swedish Threatened Species Unit, SLU.

SAS Institute (1999). *SAS online doc.* (Version 8). Cary, NC: SAS Institute.

Shugart, H. H. (2003). *A theory of forest dynamics: The ecological implications of forest succession models*. Caldwell, New Jersey: Blackburn Press.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian forests as an example. *Ecological Bulletins*, *49*, 11–41.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forest in southern Finland. *Forest Ecology and Management*, *128*, 211–225.

Sippola, A.-L. (2001). *Forest structure and biodiversity in northern boreal forests: Effects of regeneration cutting on flying beetles and wood-decomposing fungi* (Arctic Centre Reports 35). Helsinki: Hakapaino Oy.

Tonteri, T. & Siitonen, J. (2001). Lahopuu talousmetsissä valtakunnan metsien 9. inventoinnin tulosten mukaan. In J. Siitonen (Ed.), *Monimuotoinen metsä- metsäluonnon monimuotoisuuden tutkimusohjelman loppuraportti* (pp. 57–72). *Metsäntutkimuslaitoksen tiedonantoja*, 812. (In Finnish.)

Appendix 1

Core of the SAS (Release 8.2) program for obtaining the results in Tables IV and V. Notations: K_L = National park; type = Forest type; logCDW = logarithmic CDW; age = Stand age; si = Site index. Uppercase words are SAS keywords.

```
PROC MIXED DATA = Kajar4;
CLASS K_L type;
MODEL logCDW = K_L age(K_L)|age(K_L)|age(K_L) si|si|si type/HTYPE = 3;
CONTRAST 'AgeK' age(K_L) 1, age*age(K_L) 1, age*age*age(K_L) 1; * for Table IV;
CONTRAST 'AgeL' age(K_L) 0 1, age*age(K_L) 0 1, age*age*age(K_L) 0 1;
CONTRAST 'AgeK-L' age(K_L) 1 -1, age*age(K_L) 1 -1, age*age*age(K_L) 1 -1;
CONTRAST 'Site Index' si 1, si*si 1, si*si*si 1;
ESTIMATE 'K_L' K_L 1 -1; * Comparison of Karula and Lahemaa parks, for Table V;
ESTIMATE 'si 1-5' si -4 si*si -24 si*si*si -124 /CL;
ESTIMATE 'si 1-4' si -3 si*si -15 si*si*si -63/CL;
ESTIMATE 'si 1-3' si -2 si*si -8 si*si*si -26/CL;
ESTIMATE 'si 1-2' si -1 si*si -3 si*si*si -7/CL;
ESTIMATE 'si 2-5' si -3 si*si -21 si*si*si -117/CL;
ESTIMATE 'si 2-4' si -2 si*si -12 si*si*si -56/CL;
ESTIMATE 'si 2-3' si -1 si*si -5 si*si*si -19/CL;
ESTIMATE 'si 3-5' si -2 si*si -16 si*si*si -98/CL;
ESTIMATE 'si 3-4' si -1 si*si -7 si*si*si -37/CL;
ESTIMATE 'si 4-5' si -1 si*si -9 si*si*si -61/CL; RUN; QUIT;
```

II

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Assessment of tree mortality after windthrow using photo-derived data

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Köster, K., Voolma, K., Jõgiste, K., Metslaid, M. & Laarmann, D. 2009: Assessment of tree mortality after windthrow using photo-derived data. — *Ann. Bot. Fennici* 46: in press.

We used sequential surface photography and photo-derived data to evaluate tree mortality in a windthrow area in eastern Estonia, where a storm occurred in 2001. The study is based on photographs taken from the edge of three completely destroyed areas with total canopy destruction in which wind-felled spruce trees (*Picea abies*) were left after disturbance. In total, 137 spruce trees were observed over a five-year period. We used a transition matrix to examine tree mortality dynamics and patterns. At the end of the five-year period, only 25% of the spruce trees survived in areas surrounding the windthrow. The mortality was highest in the second year after disturbance and the probability of a tree falling was surprisingly high over the entire study period. According to local observations, *Ips typographus* caused most of the tree deaths, but the co-influences of other factors were also important as there was a large proportion of falling trees in the area.

Key words: *Ips typographus,* Norway spruce, *Picea abies*, repeat photography, transition matrix, windthrow

Introduction

Windstorms with windthrows play an important role in the successional cycle and dynamics of natural forests (Bouget & Duelli 2004). Windthrow increases the regional proportion of early successional and edge habitats as well as patchy open areas (Bouget & Duelli 2004). The intensity of disturbance leads to different types of opening, ranging from tree-fall gaps to stand-replacing areas. By damaging trees around larger windthrow areas and smaller gaps, windstorms even create dead-wood habitats on standing living trees, like dead branches, decaying cores and cavities (Bouget & Duelli 2004). Changes in abundance and in distribution patterns of dead wood as resources affect the abundance of insect species. Wind-felled Norway spruce (*Picea abies*) offer breeding ground for a wide range of insects and pests (Eriksson *et al*. 2005) which, in case of more severe windstorms, may lead to a population outbreak and subsequent attacks on living spruce (Schroeder 2001).

It is well known that large-scale outbreaks of the spruce bark beetle (*Ips typographus*) will develop when large numbers of fallen spruce trees are left in the forests after storms or other disturbances (Peltonen 1999, Göthlin *et al*. 2000, Nageleisen 2001, Hedgren *et al*. 2003, Meier *et al*. 2003, Okland & Berryman 2004). Generally *I. typographus* prefers to reproduce in wind-felled or otherwise damaged trees, but in some cases it is also able to damage and kill living trees in large numbers (Schroeder 2001). Several severe outbreaks are known from historical records (Schelhaas *et al*. 2003, Skuhravy 2004). Salvage logging or retention of wind-felled trees and the risk of consequential tree mortality is an important problem for forestry practice (Duelli & Obrist 1999, Wichmann & Ravn 2001, Eriksson *et al*. 2007). Due to logistical, economical and ecological reasons more and more suitable breeding material and infested trees will remain in the stands which results in increasing populations of bark beetles and their influences on standing trees (Forster 2006).

Landscape photography from a single location is used to view the typical landscape features under different environmental conditions (Dahdouh-Guebas & Koedam 2008). Some scientists have used sequential photographs to research ecosystem vegetation changes (Moseley 2006). Various methods have been used to estimate numbers of weakened, damaged or killed trees. In North America a sequential aerial photography method was used to detect trees killed by bark beetles (DeMars *et al*. 1980). Panoramic photography has been used to estimate bark beetle-killed or drought-stressed trees and to investigate other forest damage types (Caylor *et al*. 1982, Ciesla *et al*. 1982, Dillman & White 1982, Klein 1982). Recently roadside sampling was used to assess bark-beetle damage in France (Samalens *et al*. 2007).

Conventional methods such as sample plots or line transects for estimation of tree mortality in storm-disturbed areas are time consuming. Aerial surveys or mapping bark beetle infestation with high spatial resolution satellite imagery are also complicated.

In this study, we used a simple method for assessment of mortality of standing trees at the edge of heavily disturbed forest area — sequential surface photography and photo-derived data combined with local observations. Repeat photography of identical forest views is a quick and effective method for documenting changes. The key to the success of photo monitoring lies in accurately recording each step in the process and recreating the identical set up in the future (Hall 2001).

The main objective of this study was to evaluate tree mortality after windthrow. We hypothesized that weakened trees can recover to some extent during the period of observation.

Material and methods

The study areas were situated in eastern Estonia, in the Tudu Forest district (59°11´N, 26°52´E), which experienced storms on 16 July 2001. The areas are situated in the hemiboreal vegetation zone (Ahti *et al*. 1968), Norway spruce (*Picea abies*) being the dominant tree species. European aspen (*Populus tremula*), black alder (*Alnus glutinosa*), silver birch (*Betula pendula*), downy birch (*Betula pubescens*) and rowan (*Sorbus aucuparia*) were secondary tree species. The study areas included stands on eutric gleysols and calcaric cambisols (Reintam *et al*. 2001), *Filipendula* and *Myrtillus* forest site types (Lõhmus 1984) being most commonly represented (Ilisson *et al*. 2005, 2007, Köster *et al*. 2007).

No salvage logging occurred between windfall and measurements. Fieldwork was conducted in 2002, 2003, 2004, 2005 and 2006. The forest was previously under protection and no intensive management had been carried out in the area for decades. The stand ages ranged from 110 to 160 years.

The study was based on photographs taken from three completely damaged areas with total canopy destruction (all trees damaged by storm) that was the part of a larger study area. Detailed description of how the study sites where chosen has been published elsewhere (Ilisson *et al*. 2005, 2007, Köster *et al*. 2007) and the pictures used in this study are the outcome of a more extensive study program.

A Nikon D50 digital single-lens reflex camera with a 6.1 million-pixel element was used to capture the images. The camera location and photo point remained the same, as we used permanent markers for that purpose. The focal

Fig. 1. Pictures from study plot no. 5, taken in 2002 and 2005.

length was set at 18 mm to capture the maximum field of view of the plot and remained the same for all subsequent pictures. The camera was set to "Auto" to allow for automatic adjustment of aperture and shutter speed. The first picture was taken at the end of January in winter 2002, six months after disturbance. This photo image is regarded as the initial stage of measurements. The other pictures were taken in the autumns (September–October) of 2003, 2004, 2005 and 2006. Local observations were carried out to visually determine the causes of mortality.

In the first picture, we numbered every spruce that we could distinguish on the scope and later verified what changes took place in the subsequent years (Fig. 1). Multiple observers worked with first picture untill they all got the same tree count. Every year we placed each tree into one of four classes (Table 1): living tree = tree shape and crown not damaged; standing dead tree = with no needles detected; damaged tree = at least 25% decrease in crown density; fallen tree = disappeared from picture. In total 137 spruce trees were observed during the five-year period.

Table 1. Data collected from three completely damaged areas with total canopy destruction in different years.

		Number (percentage) of trees				
Plot	Year	Living	Standing dead	Damaged	Fallen	Total
1	2002	46 (82.1)	8 (14.3)	2 (3.6)	0 (0)	56
	2003	15 (26.8)	24 (42.9)	15 (26.8)	2 (3.6)	56
	2004	15 (26.8)	27 (48.2)	6 (10.7)	8 (14.3)	56
	2005	17 (30.4)	22 (39.3)	3 (5.4)	14 (25.0)	56
	2006	17 (30.4)	18 (32.1)	2 (3.6)	19 (33.9)	56
5	2002	46 (93.9)	1 (2.0)	2 (4.1)	0 (0)	49
	2003	16 (32.7)	18 (36.7)	11 (22.4)	4 (8.2)	49
	2004	19 (38.8)	22 (44.9)	4 (8.2)	4 (8.2)	49
	2005	17 (34.7)	22 (44.9)	2 (4.1)	8 (16.3)	49
	2006	14 (28.6)	21 (42.9)	0 (0)	14 (28.6)	49
9	2002	13 (40.6)	18 (56.3)	1 (3.1)	0 (0)	32
	2003	7 (21.9)	16 (50.0)	5 (15.6)	4 (12.5)	32
	2004	5 (15.6)	21 (65.6)	0 (0)	6 (18.8)	32
	2005	4 (12.5)	12 (37.5)	0 (0)	16 (50.0)	32
	2006	3 (9.4)	11 (34.4)	1 (3.1)	17 (53.1)	32

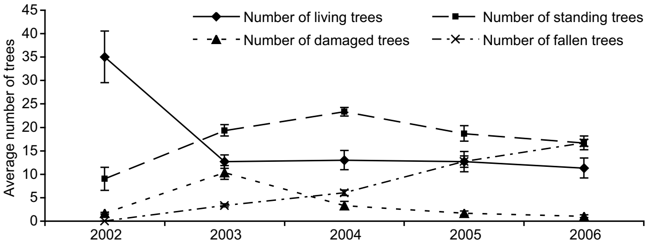

Fig. 2. Changes in average number of trees from sample plots in four different classes per year.

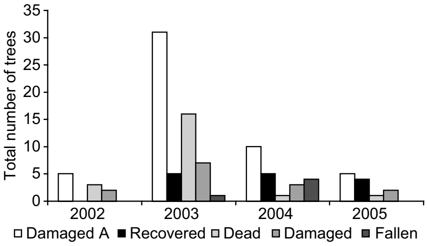

Fig. 3. Changes within damaged trees in different years after disturbance, where Damaged A represents the number of damaged trees at the beginning of the study year and other columns show the changes in those damaged trees during the year.

We used a transition matrix (Eq. 1) to determine the probabilities with which trees in different classes moved to another class. The probabilities were arranged so that the columns represented transitions from each tree state class initially present at a specific class, while the rows represented transitions to each class one time interval later. This matrix was then of the form:

$$\mathbf{A} = \begin{pmatrix} p_{11} & p_{12} & p_{13} & \cdots & p_{1n} \\ p_{21} & p_{22} & p_{23} & \cdots & p_{2n} \\ p_{31} & p_{32} & p_{33} & \cdots & p_{3n} \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ p_{n1} & p_{n2} & p_{n3} & \cdots & p_{nn} \end{pmatrix} \quad (1)$$

where p_{1n} was the probability of transition to class 1 from n time intervals. Multiplication of this matrix, $\mathbf{A}$, by a column vector $\boldsymbol{x}_t$ that describes the tree state class at time t gives the tree state class at time $t + 1$.

We also used the chi-square (χ^2) test to see if the transition matrices were statistically different in different years.

Results

The results of this study allowed us to predict five-year dynamics after disturbance. During this period, approximately 25% of the spruces survived in areas surrounding the windthrow (not totally damaged by storm). On average, only 11 trees per plot out of 35 survived (Fig. 2). We found the largest number of damaged trees (more than 22% on average) in the second year after disturbance (Table 1 and Fig. 2). The number of damaged trees started to decrease later and, while most of those trees died, some recovered and continued as living trees (Fig. 3). The transition probability matrix demonstrated that most of the damaged trees died during the second year after disturbance, but some recovered (Table 2 and Fig. 3). After a longer time after the disturbance — in the third and fourth years — the relative number of trees recovering was remarkably high (more than 50% of the damaged trees recovered; Fig. 3).

The number of standing dead trees increased until the third year after disturbance (Fig. 2). The number of standing dead trees later decreased, as these were starting to fall. It can be suggested that the probability of a standing dead tree falling down was greatest at the end of the fourth year, but in general a considerable number of standing dead trees fell each year (Table 2).

The most rapid change in the number of living trees took place during the second year after disturbance (Figs. 2 and 4), but this number remained stable later. During those rapid changes in the number of living trees, most trees were damaged or already standing dead trees, but some living trees fell as well (Fig 4).

Some interesting patterns emerged from examination of the transition matrices (Table 2).

A remarkably high recovery of damaged trees was observed every year. The probability of a tree falling was surprisingly high during the entire five-year study period.

Discussion

The results of our study followed the same pattern as reported in earlier papers, in which the mortality in the areas studied was highest in the second or third summer following the storm disturbance (Schroeder 2001, Bouget & Duelli 2004, Eriksson *et al*. 2007). In our study, almost half of the tree deaths were recorded in the second year following the wind felling. These tree deaths were probably caused by *I. typographus,* as it came out from local observations that all the dead spruce trees were colonized by it, although the analysis of sequential photographs is often limited to visual inspection and it is hard to determine the exact cause of tree death.

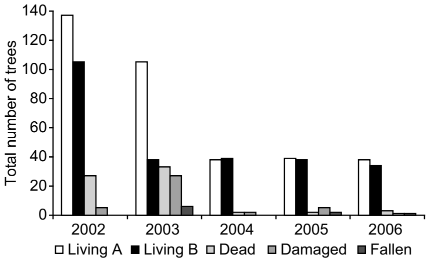

Fig. 4. Changes within living trees in different years after disturbance, where Living A represents the number of living trees at the beginning of the study year and other columns represent the changes in those living trees during the year.

About 1.5 million m^3 of wood was damaged by local windstorms in 2001 and 2002, but as timber was removed in time, no extensive outbreaks of bark beetles in the commercial forests followed. However, quite a different situation was observed in the protected forests of nature reserves, where the storm-damaged trees were

Table 2. Transition probability matrices. The columns represent transitions from each class initially at time *t*, while the rows represent transitions to each class one time interval later ($t + 1$). Differences between matrices were tested with a χ^2-test.

	Trees			
	Living	Damaged	Fallen	Standing dead
Number of trees in 2002	105	5	0	27
2002–2003 $p < 0.0001$				
Living	0.277	0.000	0.000	0.000
Damaged	0.204	0.015	0.000	0.000
Fallen	0.044	0.000	0.000	0.036
Standing dead	0.241	0.022	0.000	0.161
2003–2004 $p < 0.0001$				
Living	0.248	0.036	0.000	0.000
Damaged	0.015	0.058	0.000	0.000
Fallen	0.000	0.007	0.073	0.007
Standing dead	0.015	0.117	0.007	0.372
2004–2005 $p < 0.0001$				
Living	0.219	0.036	0.000	0.000
Damaged	0.036	0.022	0.000	0.000
Fallen	0.015	0.007	0.131	0.124
Standing dead	0.015	0.007	0.000	0.387
2005–2006 $p < 0.0001$				
Living	0.219	0.036	0.000	0.000
Damaged	0.007	0.015	0.000	0.000
Fallen	0.007	0.000	0.277	0.073
Standing dead	0.022	0.007	0.000	0.336

left untouched. This led to an increase in the bark beetle populations and resulted in extensive beetle-induced tree mortality in neighbouring spruce stands. Damage by spruce bark beetles occurs mainly in eastern Estonia (Nilson *et al*. 1999), where spruce stands grow in site types where soil humidity depends directly on the amount of precipitation. Some studies found that in very hot summers, as in 2001 and 2002, *I. typographus* prefers the cooler inner parts of the stands for breeding rather than sun-exposed open habitats (Eriksson *et al*. 2007). Bark beetles generally prefer wind-felled or otherwise damaged spruce trees (Schroeder 2001, Eriksson *et al*. 2007), but most wind-felled trees become unsuitable as breeding-ground a year or two after disturbance (Bouget & Duelli 2004) and bark beetles are confined to attacking living trees on the surrounding edges (Peltonen 1999, Schroeder 2001). The list of bark beetles of Estonia includes 68 species (Voolma *et al*. 2000), but only a few can attack growing trees and pose a real threat to forests. Bark beetles of the *Ips* genus belong to those that can affect forests most. Of the five species of this genus occurring in Estonia, three (*Ips typographus, I. duplicatus, I. amitinus*) inhabit Norway spruce. All these species, as well as an accompanying species, *Pityogenes chalcographus*, were recorded in the study area when the local observation was carried out.

The probability of a dead standing tree falling and for a living tree falling was surprisingly high during the entire five-year study period. This quite early falling of standing dead trees made it seem that not all spruces were killed by bark beetles. Here we can probably consider the co-influence of various disturbance types. The root systems of living spruces were probably damaged by storms or fungi, thus weakening the trees. Bark beetles killed the trees and these standing dead spruces fell so early because of their damaged root system. It usually takes some decades for standing dead trees to fall because of decomposition (Storaunet & Rolstad 2002, 2004, Storaunet 2004), mainly because of drying out after death (Krankina & Harmon 1995). The same pattern was also observed in our storm-damaged areas (stands totally and partially damaged by wind) where broken spruce stems are still standing (K. Köster unpubl. data). Therefore we assume that trees survived the storm, but that their root systems were damaged, weakening them. The co-influence of storm damage and bark beetle attacks made the trees die quickly and they blew down with the next strong winds. The repeated storm events cause complex patterns of tree mortality. Eriksson *et al*. (2007) found that older standing trees seem to be more susceptible to *I. typograpus* attacks than younger ones. In our study, the stand ages ranged from 110 to 160 years, and this may also be a factor causing high mortality among trees that survived the wind damage.

Seasonal aspects are also important. The time of year when trees are windthrown also influences the level of colonization by beetles (Bouget & Duelli 2004, Eriksson *et al*. 2007). Trees falling in winter provide less decay products attractive to beetles than trees falling in autumn (Schroeder *et al*. 1999). The winter conditions with frozen ground also reduce the risk of damage to roots.

It is possible that other factors besides partial damage and associated bark beetle attacks are responsible for tree death. An altered water regime or temperature fluctuations in open conditions may increase susceptibility to bark beetle attacks or infection by fungi (Harmon *et al*. 1986, Storaunet & Rolstad 2002, 2004, Storaunet 2004).

Management decisions are crucial in planning forests. Salvage logging is a decision often made by managers after disturbance because of the fear of insect outbreaks and fire hazard (Stanturf *et al*. 2007). The question of salvaging partially damaged areas is also unanswered. With heavy destruction, the problem of the surviving trees remains. We may also imagine that if the border between damaged and surviving stands is strict, it might mean that the survival of an undamaged stand is better since they are in good condition. In a situation where we have a half-damaged area between damaged and surviving stands, however, it might be a good idea to remove the half-damaged stand.

Wichmann and Ravn (2001) observed that the density of attacks on standing trees around windthrown trees correlates with the time of salvage harvesting. Removal of fallen trees before the first spring may further inhibit local infestations. In this case, living trees are used as bait trees, since they are attractive to the hibernating beetles and natural enemies of beetles emerge from spruce logs one or two months after the spruce bark beetles (Wermelinger 2002). Foresters should thus focus on sanitation fellings of newly-attacked living trees and leave the older stems and standing dead trees for the benefit of saproxylics and natural enemies (Wermelinger 2002). On the other hand, the decision to leave a part unsalvaged may be essential to protect other resource values (Stanturf *et al*. 2007). Areas with regeneration due to excessive game browsing may benefit from coarse woody debris created after a storm (de Chantal & Granström 2007) or its delayed formation.

Monitoring of bark-beetle damage is often problematic and efforts are being made to estimate damage extent more extensively and precisely. Many large-scale outbreaks of spruce bark beetles have been reported in Estonia over the last two centuries, in 1868–1874, 1880–1886, 1897–1902, 1912–1915, 1924–1929, 1934–1940, 1968–1973, and 1992–1995 (Voolma 1998, Voolma *et al*. 2000, Wichmann & Ravn 2001, Voolma 2002). Various natural disturbances in forests have usually preceded the outbreaks: a hot summer and big forest fires in 1868, snow breaks in 1879–1880 and 1911, storm damage in 1923, 1938, 1943, 1967 and 1969, and drought in 1882, 1934–1935 and 1992. The heaviest storm in Estonia occurred in August 1967, devastating about 6 million m^3 of forest, with trees downed and uprooted along the storm path. The ensuing damage caused by bark beetles exceeded 2 million m^3 (Mihkelson 1998). Since some countries now have the goal of retaining biodiversity by leaving more and more wind-felled trees in the managed forest (Schroeder 2001), it is important to evaluate the risk of damage caused by the wind, bark beetles and other factors, and repeat photography definitely qualifies as a cheap and accessible data source.

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References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Annales Botanici Fennici* 5: 169–211.

Bouget, C. & Duelli, P. 2004: The effects of windthrow on forest insect communities: a literature review. — *Biological Conservation* 118: 281–299.

Caylor, J., Pierce, J. & Salazar, W. 1982: Optical bar panoramic photography for planning timber salvage in drought-stressed forests. — *Photogrammetric Engineering and Remote Sensing* 48: 749–753.

Ciesla, W. M., Allison, R. A. & Weber, F. P. 1982: Panoramic aerial-photography in forest pest-management. — *Photogrammetric Engineering and Remote Sensing* 48: 719–723.

Dahdouh-Guebas, F. & Koedam, N. 2008: Long-term retrospection on mangrove development using transdisciplinary approaches: a review. — *Aquatic Botany* 89: 80–92

de Chantal, M. & Granström, A. 2007: Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. — *Forest Ecology and Management* 250: 3–8.

DeMars, C. J., Slaughter, G. W., Bedard, W. D., Norick, N. X. & Roettgering, B. 1980: Estimating western pine beetle-caused tree mortality for evaluating an attractive pheromone treatment. — *Journal of Chemical Ecology* 6: 853–866.

Dillman, R. D. & White, W. B. 1982: Estimating mountain pine beetle-killed ponderosa pine over the front range of Colorado with high-altitude panoramic photography. — *Photogrammetric Engineering and Remote Sensing* 48: 741–747.

Duelli, P. & Obrist, M. K. 1999: Räumen oder belassen? Die Entwicklung der faunistischen Biodiversität auf Windwurfflächen im schweizerischen Alpenraum. — *Verhandlungen der Gesellschaft für Ökologie* 29: 193–199.

Eriksson, M., Pouttu, A. & Roininen, H. 2005: The influence of windthrow area and timber characteristics on colonization of wind-felled spruces by *Ips typographus* (L.). — *Forest Ecology and Management* 216: 105–116.

Eriksson, M., Neuvonen, S. & Roininen, H. 2007: Retention of wind-felled trees and the risk of consequential tree mortality by the European spruce bark beetle *Ips typographus* in Finland. — *Scandinavian Journal of Forest Research* 22: 516–523.

Forster, B. 2006: Climate change and management change: the response of forest insects in Switzerland. — In: Csoka, G., Hirka, A. & Koltay, A. (eds.), *Biotic damage in forests. Proceedings of the IUFRO (WP 7.03.10) Symposium held in Matrafüred, Hungary, September 12–16, 2004*: 41–53. Hungarian Forest Research Institute, Matrafüred.

Göthlin, E., Schroeder, L. M. & Lindelöw, A. 2000: Attacks by *Ips typographus* and *Pityogenes chalcographus* on windthrown spruces (*Picea abies*) during the two years following a storm felling. — *Scandinavian Journal of Forest Research* 15: 542–549.

Hall, F. C. 2001: *Photo point monitoring handbook. Part A: field procedures*. — General technical report, Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland Oregon, U.S. PNW-GTR-526.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W. K., Cromack, J. & Cummins, K. W. 1986: Ecology of coarse woody debris in temperate ecosystems. — *Advances in Ecological Research* 15: 133–302.

Hedgren, P. O., Schroeder, L. M. & Weslien, J. 2003: Tree killing by *Ips typographus* (Cleoptera: Scolytidae) at stand edges with and without colonized felled spruce trees. — *Agricultural and Forest Entomology* 5: 67–74.

Ilisson, T., Köster, K., Vodde, F. & Jõgiste, K. 2007: Regeneration development 4–5 years after a storm in Norway spruce dominated forests, Estonia. — *Forest Ecology and Management* 250: 17–24.

Ilisson, T., Metslaid, M., Vodde, F., Jõgiste, K. & Kurm, M. 2005: Storm disturbance in forest ecosystems in Estonia. — *Scandinavian Journal of Forest Research* 20 (Suppl. 6): 88–93.

Klein, W. H. 1982: Estimating bark beetle-killed lodgepole pine with high-altitude panoramic photography. — *Photogrammetric Engineering and Remote Sensing* 48: 733–737.

Krankina, O. N. & Harmon, M. E. 1995: Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. — *Water, Air and Soil Pollution* 82: 227–238.

Köster, K., Ilisson, T. & Jõgiste, K. 2007: Nutrients in coarse woody debris and forest regeneration in windthrow areas. — *Miškininkyste* 1(61) Suppl. 1: 13–18.

Lõhmus, E. 1984: *Eesti metsakasvukohatüübid*. — ENSV ATK IJV, Tallinn.

Meier, F., Gall, R. & Forster, B. 2003: Ursachen und Verlauf der Buchdrucker-Epidemien (*Ips typographus* L.) in der Schweiz von 1984 bis 1999. — *Schweizerische Zeitschrift für Forstwesen* 154: 437–441.

Mihkelson, S. 1998: Forest health condition. — In: Etverk, I. (ed.), *Sajandi suurtormid Eesti metsades*: 27–34. Eesti Metsaselts.

Moseley, R. K. 2006: Historical landscape change in northwestern Yunnan, China — using repeat photography to assess the perceptions and realities of biodiversity loss. — *Mountain Research and Development* 26: 214–219

Nageleisen, L.-M. 2001: Monitoring of bark and wood-boring beetles in France after the December 1999 storms. — *Integrated Pest Management Reviews* 6: 159–162.

Nilson, A., Kiviste, A., Korjus, H., Mihkelson, S., Etverk, I. & Oja, T. 1999: Impact of recent and future climate change on Estonian forestry and adaptation tools. — *Climate research* 12: 205–214.

Okland, B. & Berryman, A. 2004: Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. — *Agricultural and Forest Entomology* 6: 141–146.

Peltonen, M. 1999: Windthrows and dead-standing trees as bark beetle breeding material at forest-clearcut edge. — *Scandinavian Journal of Forest Research* 14: 505–511.

Reintam, L., Rooma, I. & Kull, A. 2001: Map of soil vulnerability and degradation in Estonia. — In: Stott, D. E., Mohtar, R. H. & Steinhard, G. C. (eds.), *Sustaining the global farm, 10th International Soil Conservation Organization Meeting, USDA-ARS NSERL, May 24–29, 1999*: 1068–1074. Purdue University.

Samalens, J. C., Rossi, J. P., Guyon, D., Van Halder, I., Menassieu, P., Piou, D. & Jactel, H. 2007: Adaptive roadside sampling for bark beetle damage assessment. — *Forest Ecology and Management* 253: 177–187.

Schelhaas, M.-J., Nabuurs, G.-J. & Schuck, A. 2003: Natural disturbances in the European forests in the 19th and 20th centuries. — *Global Change Biology* 9: 1620–1633

Schroeder, L. M. 2001: Tree mortality by the bark beetle *Ips typographus* (L.) in storm-disturbed stands. — *Integrated Pest Management Reviews* 6: 169–175.

Schroeder, L. M., Weslien, J., Lindelöw, Å. & Lindhe, A. 1999: Attacks by bark- and wood-boring Coleoptera on mechanically created high stumps of Norway spruce in the two years following cutting. — *Forest Ecology and Management* 123: 21–30.

Skuhravy, V. [Скухравы, В.] 2004: [Outbreaks of mass reproduction of *Ips typographus* in Europe in XIV–XX centuries]. — *International Organization for Biological Control of Noxious Animals and Plants, East Palaearctic Section, Bulletin* 4: 95–117. [In Russian].

Stanturf, J. A., Goodrick, S. L. & Outcalt, K. W. 2007: Disturbance and coastal forests: a strategic approach to forest management in hurricane impact zones. — *Forest Ecology and Management* 250: 119–135.

Storaunet, K. O. 2004: Models to predict time since death of *Picea abies* Snags. — *Scandinavian Journal of Forest Research* 19: 250–260.

Storaunet, K. O. & Rolstad, J. 2002: Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. — *Canadian Journal of Forest Research* 32: 1801–1812.

Storaunet, K. O. & Rolstad, J. 2004: How long do Norway spruce snags stand? Evaluating four estimation methods. — *Canadian Journal of Forest Research* 34: 376–383.

Wermelinger, B. 2002: Development and distribution of predators and parasitoids during two consecutive years of an *Ips typographus* (Col., Scolytidae) infestation. — *Journal of Applied Entomology* 126: 521–527.

Wichmann, L. & Ravn, H. P. 2001: The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. — *Forest Ecology and Management* 148: 31–39.

Voolma, K. 1998: A review of the history of forest entomology in Estonia. — *Teaduse ajaloo lehekülgi Eestist* 12: 140–158. [In Estonian with English summary].

Voolma, K. 2002: Health condition of Estonian forests in the 1920–1930s. — *Proceedings of the Estonian Academic Forest Society* 17: 61–71. [In Estonian with English summary].

Voolma, K., Õunap, H. & Süda, I. 2000: *Scolytidae. Distribution maps of Estonian insects, 2*. — Eesti Loodusfoto, Tartu.

III

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RAPID EFFECTS AFTER FOREST DISTURBANCE IN DECOMPOSITION OF TREES IN TWO WINDTHROWN AREAS IN EAST ESTONIA.
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Rapid 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). 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). Initial wood densities were different, depending on tree species, log or snag position (lying, 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. Lying 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.

Keywords: 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, a habitat for a wide array of organisms, and after humification it is an important component of forest soil (Siitonen 2001).

Previous studies 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 in initially similar habitats/conditions but with a different severity of damage can be completely different.

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 decay as change in wood density. 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. It was hypothesized: (1) CWD under a partial overstory (partly damaged) decays faster due to better microclimate. (2) birch decays faster than spruce because of wood characteristics 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 +5.2 ^{o}C. The coldest month is February, at -5.7^{o}C and the warmest is July at +16.4 ^{o}C. 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).

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 (m3/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

No salvage loggings 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 preserve) where there has been no management intervention in decades. The stand ages 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 even among the Norway spruce and birch.

Randomly selected sample trees for measuring the decomposition processes 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 lying or leaning) were randomly selected from spruce (*Picea abies* L. Karst) and birch (*Betula* s*pp.*).

Field and laboratory measurements

Sampled living trees and CWD 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 in order to get four wood subsamples form 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 1g). Wood subsamples (ca 20 g) were taken from each disk, weighted and air-dried in paper bags to stop decomposition. The cores were taken from different locations on the disk depending on its diameter, as shown in Figure 1. The data set for analyses included a total of 944 subsamples from 174 spruces and 160 birches.

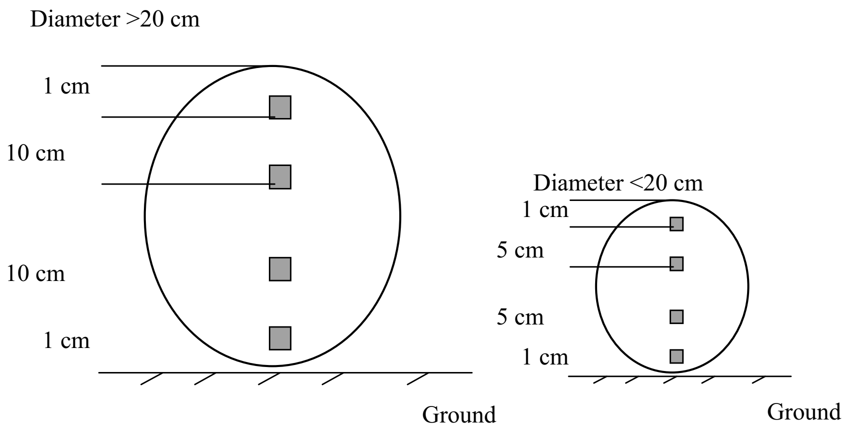

Figure 1. The location of subsamples depended on disk diameter. On disks with diameter >20 (diameter without bark) the cores were taken at 1 cm from the edge of the disk and at 10 cm from the edge of the disk. On disks with diameter <20 (minimum 12 cm), the cores were taken at 1 cm and at 5 cm from the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

Dry mass of cores was measured after oven drying at 65°C to the 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 g cm^{-3}, the weight of the displaced water equals the volume of the sample. The basic density (d, in g cm^{-3}) of each sample was calculated by the formula

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

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

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 (cores 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 core position in the core 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. 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 (it obtains for both tree species).

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	Lying	16	0.493 (0.013)	TD	Spruce	Lying	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	Lying	16	0.495 (0.016)	PD	Spruce	Lying	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	Lying	12	0.581 (0.024)	TD	Birch	Lying	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	Lying	8	0.669 (0.032)	TD	Birch	Lying	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)

The mean CWD density decrease, both in spruce and birch, 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 lying 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 ranged 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 lying 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 third decay class. In 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 – lying, leaning or standing, Disk position – position of the sample disk on the trunk (three positions for a tree), Core position – position of the core sample on the sample disk (see Figure1), 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 cores on the sample disk (Figure 1): σ^2_ε is the residual variance of LDensity and ρ is the correlation between the adjacent cores 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 No	Factor (type)	Nested/ Grouped within	DF	ANOVA Type or Covariance parameter	Major factors in Type I Analysis	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 (F)	1, 4	14/188	I, III	1, 2, 4	n.s.
8	6	Core position: birch (R)	0, 1	–	AR(1)	–	n.s.
9	6	Core position: spruce (R)	0, 1	–	AR(1), ρ = –0.37	–	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

The results of our study revealed that the wood decay (wood density changes) was also dependent on log or snag position (Table 3 Row 5). Ranking wood density by log or snag position we got Figures 2 and 3 which indicated that lying 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 enables to explain this dependence also with the impact of other factors apart from snag/log position. In case of spruce, lying logs were decaying faster (loosing density) in all areas with different damage severity (Figure 2). The same tendency was observed in case of birch, where lying logs were loosing their density faster than leaning and standing logs/snags (Figure 3).

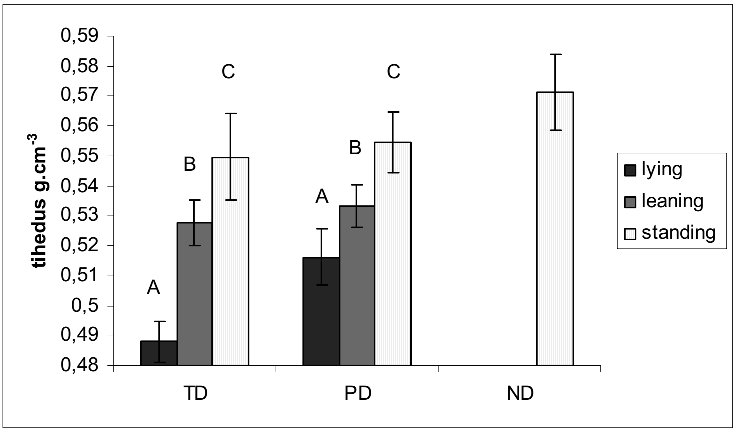

Figure 2. The wood density in lying, leaning and standing spruce logs/snags on totally and partly damaged areas compared with living tree density. Where TD means totally damaged area, PD means partly damaged area and ND means control area with no damage. Error bars show standard deviation and statistically significant differences denoted by different letters above bars.

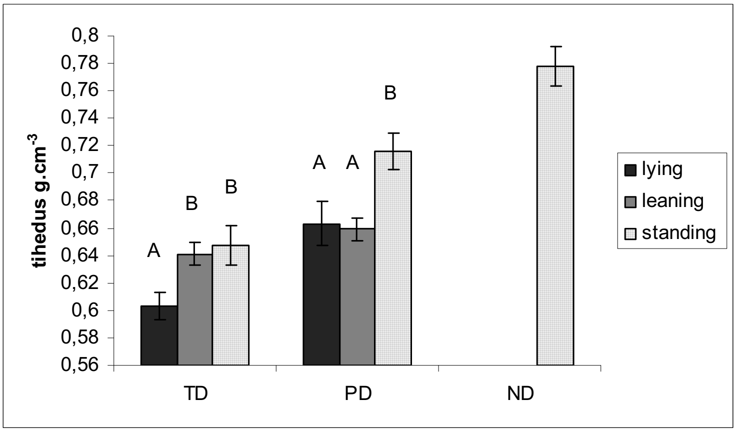

Figure 3. The wood density changes in lying, leaning and standing birch logs/snags on totally and partly damaged areas compared with living tree density. Where TD means totally damaged area, PD means partly damaged area and ND means control area with no damage. Error bars show standard deviation and statistically significant differences denoted by different letters above bars.

Several rows (Rows 7, 8, 9) in Table 3 present the effects of core 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 core 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 null hypothesis and, therefore, the effect of disk position was not proved. The other factor was the core 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 margin of the spruce core disk to the lower margin, density changes could be observed and lower margin 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 first decay class have been decaying on average 1.6 years and log/snags that are in second Decay class have been decaying on average 3.3 years. Spruce logs that are in first decay class have been decaying on average 3.1 years and logs/snags that are in second. decay class have been decaying on average 6.5 years.

Decay 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 decaying 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 decay (Hytteborn and Packham 198,; Næsset, 1999, Shorohova and Shorohov 2001, Macensen 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 our case, at the beginning of the decay processes, lying 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 improves moisture level inside the log. Hytteborn and Packham (1987) and Næsset (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 decay 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 here can be that after disturbance in TD area the transpiration capacity of trees is low or is absent and the areas will become wet. So as the moisture level stays high, the wood material is not drying/seasoning through and in these warm and moist conditions are 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, 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 in average the proportion of uprooting and stem breakage was relatively even. In our study we also tested the effect of time. As the intensity 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 and calculations for decay rate were not made. The 3-year decay period is too short to estimate the long-term decomposition rate.

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 and it is at its lowest in mid-age stages. 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 damages and will die later (finally death is caused by other factors, such as insects, fungi *etc.*).

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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

References

Ahti, T., Hämet-Ahti, L. and Jalas, J. 1968. Vegetation zones and their sections in the northwestern Europe. *Ann. Bot. Fen*. 5: 169-211.

Angelstam, P.K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sc*i. 9: 593-602.

Arsenault, A. 2002. Managing Coarse Woody Debris in British Columbia's Forests: A Cultural Shift for Professional forester? pp 869-878 In: Laudenslayer, W.F., Shea, P. J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E., technical coordinators. Proceedings of the symposium on the ecology and management of dead wood in western forests. 1999 November 2-4; Reno, NV. Gen. Tech. Rep. PSW-GTR-181. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 949 p.

Boddy, L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. *Ecol. Bull*. 49: 43-56.

Esseen, P-A., Ehnström, B., Ericson, L. and Sjöberg, K. 1992. Boreal forests- the focal habitats of Fennoscandia. – In: Hansson, L. (ed.), Ecological principles of nature conservation. Applications in temperate and boreal environments. *Elsevier Science Publishers,* London, p. 252-325.

FAO, ISSS, ISRIC. 1998. World reference base for soil resources. World Soil Resources Rep. 84, Rome.

Haila, Y., Hanski, I.K., Niemelä, J., Punttila, P., Raivio, S. and Tukia, H. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. *Ann. Zool. Fen*. 31: 187-202.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr. and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15: 133-302.

Harmon, M.E., Krankina, O.N. and Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Can. J. For. Res*. 30: 76-84.

Hytteborn, H. and Packham, J.R. 1987. Decay rate of Picea abies logs and the storm gap theory: a re-examination of Sernander Plot III, Fiby urskog, central Sweden. *Arboricult. J.* 11: 299-311.

Ilic, J., Boland, D., McDonald, M., Downes, G. and Blakemore, P. 2000. Woody density phase 1 - state of knowledge. In, National Carbon Accounting System Technical Report No. 18. Australian Greenhouse Office, Canberra.

Ilisson, T., Metslaid, M., Vodde, F., Jõgiste, K. and Kurm, M. 2005. Storm disturbance in forest ecosystems in Estonia. *Scan. J. For. Res*. 20 (Suppl 6): 88-93.

Karjalainen, L. and Kuuluvainen, T. 2002. Amount and diversity of coarse woody debris within a boreal forest landscape dominated by Pinus sylvestris in Vienansalo wilderness, eastern Fennoscandia. *Silva Fenn.* 36(1): 147-167.

Krankina, O.N. and Harmon, M.E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. *Water Air Soil Pollut.* 82: 227-238.

Krankina, O.N., Harmon, M.E. and Griazkin, A.V. 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. *Can. J. For. Res*. 29: 20-32.

Krankina, O.N., Harmon, M.E., Kukuev, Y.A., Treyfeld, R.F., Kashpor, N.N., Kresnov, V.G., Skudin, V.M., Protasov, N.A., Yatskov, M., Spycher, G. and Povarov, E.D. 2002. Coarse woody debris in forest regions of Russia. *Can. J. For. Res.* 32: 768-778.

Kuuluvainen, T., Tukia, H. and Aapala, K. 2005. Ecological restoration of forested ecosystems in Finland. In: Stanturf, J.A. & Madsen, P. (eds.), Restoration of boreal and temperate forests. pp 285-298. Boca Ration, FL: CRC Press.

Laiho, R. and Prescott, C.E. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Can. J. For. Res*. 34: 763-777.

Linder, P. and Östlund, L. 1998. Structural changes in three midboreal Swedish forest landscapes, 1885-1996. *Biol. Conserv*. 85: 9-19.

Lõhmus, E. 1984. Eesti metsakasvukohatüübid. (Estonian forest site types). Tallinn: ENSV ATK IJV. (In Estonian).

Mackensen, J. and Bauhus, J. 1999. The decay of coarse woody debris. National Carbon Accounting System technical report; No. 6. Australian Greenhouse Office, Commonwealth of Australia, Canberra.

Næsset, E. 1999. Decomposition rate constants of *Picea abies* in southeastern Norway. *Can. J. For. Res*. 29: 372-381.

Niemelä, J. 1996. Invertebrates and the boreal forest management. *Conserv. Biol*. 11: 601-610.

Reintam, L., Rooma, I. and Kull, A. 2001. Map of soil vulnerability and degradation in Estonia. In: D.E. Stott, R.H. Mohtar and G.C. Steinhardt, Editors, Sustaining the Global Farm. Selected papers from the 10th International Soil Conservation Organization Meeting held May 24–29, 1999, Purdue University, USDA-ARS NSERL, p. 1068–1074.

Renvall, P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in the northern Finland. Karstenia 35: 1-51.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. pp 17-33 in The ecology of natural disturbances and patch dynamics, Pickett, S.T.A. and White, P.S. (eds). Academic Press, Inc. Orlando, FL. 472 p.

Samuelsson, J., Gustafsson, L. and Ingelög, T. 1994. Dying and dead trees- a review of their importance for biodiversity. - Swedish threatened species unit, SLU. Uppsala, 109 p.

SAS Institute Inc. 1999. SAS OnlineDoc., (Version 8). Cary, NC: SAS Institute Inc.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49: 11-14.

Shorohova, E.V. and Shorohov, A.A. 2001. Coarse woody debris dynamics and stores in a boreal virgin spruce forests. *Ecol. Bull.* 49: 129-135.

Tarasov, M.E. and Birdsey, R.A. 2001. Decay rate and potential storage of coarse woody debris in the Leningrad Region. *Ecol. Bull*. 49: 137-147.

Tukia, H., Jaakola, S. and Lindholm, T. 2001. Metsien luonnontilaisuuden ja ennallistamistarpeen arviointi Lahemaan ja Karulan kansallispuistossa. Tutkimusraportti.

(The assessment of naturality and the need of restoration in Lahemaa and Karula National Parks. Scientific report.) In: Ennallistamisen käyttö Viron luonnonsuojelualueilla, Tiedotus- ja kehittämishanke 2000-2001 (The restoration practice in Estonian nature conservation areas 2000-2001). EKAL, Metsähallitus Consulting, Soumen Ympäristökeskus.

Yatskov, M., Harmon, M.E. and Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. *Can. J. For. Res*. 33: 1211-1226.

IV

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REGENERATION DEVELOPMENT 4-5 YEARS
AFTER A STORM IN NORWAY SPRUCE
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Regeneration development 4–5 years after a storm in Norway spruce dominated forests, Estonia

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Abstract

The regeneration patterns in wind-damaged areas are largely influenced by damage severity and varied microrelief. Regeneration was studied in *Picea abies* dominated stands with total and partial canopy destruction and in harvested areas in *Myrtillus* and *Filipendula* site types in Estonia 4–5 years after a storm, examining particularly the influence of microsites on regeneration establishment and growth. The seedling densities of regeneration were highest in harvested plots compared to heavily and moderately damaged areas. The seedling densities were lowest on mounds and highest in pits among microsites in heavily and moderately damaged sites. The most common tree species regenerating in pits were birch (*Betula pendula* Roth., *Betula pubescens* Ehrh.) and alder (*Alnus glutinosa* (L.) J. Gaertn.). Birch and alder seedlings that survived to 2005 were taller in 2004 than those that died. Trees were also taller with lower regeneration density. Spruces (*Picea abies* (L.) Karst.) did not prefer any particular microsite, but those growing in pits were smaller than those in other microsites. The plots harvested regenerate more rapidly with hardwood species.

Keywords: Windthrow; Regeneration; Pit and mound; Wind severity; Microsite

1. Introduction

Windthrow is an important driver of gap dynamics in European temperate and boreal forest ecosystems (Ulanova, 2000). The consequences of wind disturbance can be quite varied, depending on forest structure and composition and the characteristics of each storm (Lindemann and Baker, 2001). One of these characteristics, disturbance severity, may however provide a way to organize such daunting variation among disturbances. Indeed, in at least two recent conceptual models of forest disturbance and recovery, those of Frelich (2002) and Roberts (2004), severity is one of the primary axes for differentiating disturbance effects. Disturbance severity determines which component of pre-disturbance vegetation survives or is killed. Consequently, severity can influence regeneration in two ways: (1) the physical change in light and nutrient availability; (2) the availability of seed trees, seedbanks or advance regeneration for seedling establishment.

Regeneration via seed in storm-damaged areas depends on patches suitable for germination, establishment, and survival (Ulanova, 2000; Ruel and Pineau, 2002). Environmental conditions within the gap vary greatly, and can positively or negatively influence each of these stages. Light availability, for example, increases most north of gap center (in the northern hemisphere, De Chantal et al., 2003), which could alter the community structure (Hytteborn and Packham, 1987; Dyer and Baird, 1997; Drobyshev, 2001). Uprooted trees increase environmental heterogeneity because of the creation of a pit–mound microtopography by the relocated root systems and because of the freed space on the forest floor (Greenberg and McNab, 1998; Ulanova, 2000). Pits, defined as the areas where mineral soil has become exposed; mounds, defined as the rootplates that have turned into a vertical position; intact, forest floor and decaying logs provide areas with very different microclimates and conditions (Peterson et al., 1990; Bazzaz, 1996; DeLong et al., 1997; Clinton and Baker, 2000; Peterson and Pickett, 2000; Ulanova, 2000; Ruel and Pineau, 2002), which in turn may increase biodiversity at the stand level (Lässig and Močalov, 2000; McAlister et al., 2000).

An important management question after windstorms is whether to leave or harvest the windthrown trees. General forestry practice prescribes salvage harvesting after heavy storm damage because of the fear of insect outbreaks and fire hazard. Both natural and artificial regeneration has also been

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thought to establish more efficiently on cleared sites (Karr et al., 2004; Beschta et al., 2004). However, the validity of such assumptions has recently been questioned in North America (Lindenmayer et al., 2004; Donato et al., 2006), generating much controversy.

Our objective in this study was to find out how disturbance severity and management influence recovery. The following hypotheses were formulated: (1) in accordance with the site heterogeneity, recruitment tree species diversity is greater in uncleared areas; (2) small-seeded species germinate better in exposed mineral soil (pits and mounds), large-seeded species need a more stable environment (intact soil); (3) pioneer species establish and grow better in more severely damaged areas, cleared areas, on mounds and to a certain extent in pits, while shade-tolerant species prefer uncleared, partly damaged areas and vegetated intact forest floor; (4) because of soil instability, seedlings on mounds will show the highest mortality figures; (5) in addition to soil stability, seedling survival depends on the individual's height and seedling densities.

2. Material and methods

The study areas are situated in Tudu (59°11′N, 26°52′E) and Halliku Forest Districts (58°43′N, 26°55′E) in Eastern Estonia. Thunderstorms occurred in Tudu in July 2001 and Halliku in July 2002, the amounts of dead wood reaching over 600 m^3 per hectare (Ilisson et al., 2005a). In both areas Norway spruce (*Picea abies* (L.) Karst.) dominates in mixed forests. Accompanying tree species are silver and downy birch ((*Betula pendula* Roth. and *Betula pubescens* Ehrh.), European aspen (*Populus tremula* L.) and black alder (*Alnus glutinosa* (L.) J. Gaertn.). Both Forest Districts are located in flat land and influenced by drainage. The study areas were established in the *Myrtillus* and *Filipendula* site types (Lõhmus, 2004). The *Myrtillus* site type is most commonly represented in Estonia (approximately 20% of the state forest area), while the *Filipendula* site type makes up approximately 5% of the state forest area (Lõhmus, 2004). Gley and gleyed podzolic soils occur in both Forest Districts. The age of the stands varied between 110 and 160 years. Previous publications concerning the study areas consider post-disturbance forest structure (Ilisson et al., 2005a), the decomposition dynamics of dead wood (Köster, 2005) and understorey vegetation dynamics (Ilisson et al., 2006).

Data from 12 study plots (40 m long × 20 m wide) were used, the plots being located in areas of three different disturbance severity classes—the areas with (i) partial canopy destruction (moderately damaged), (ii) total canopy destruction (heavily damaged) and (iii) areas that were logged after wind damage (harvested). The heavily and moderately damaged study plots were established in protected compartments (dead wood was left on site); and the logged plots were in the surrounding management forests of the Tudu and Halliku Forest Districts. Each "treatment" had four replicate transects. The plots were established a year after the storms.

Rubus saxatilis, *Oxalis acetosella*, *Athyrium filix-femina*, *Hepatica nobilis*, *Geum rivale* and *Vaccinium myrtillus* were most abundant herb-layer species in 2004 in moderately damaged study plots. In heavily damaged areas, *Thelypteris phegopteris*, *Oxalis acetosella*, *Epilobium montanum*, *Rubus saxatilis* and *Vaccinium myrtillus* dominated the herb layer. *Epilobium angustifolium*, *Rubus idaeus*, *Ranunculus repens* and *Epilobium montanum* dominated in harvested plots (Ilisson et al., 2006). In the moss layer, *Rhytidiadelphus triquetrus*, *Plagiomnium* spp., *Hylocomium splendens*, *Pleurozium schreberi* and *Sphagnum* spp. dominated in heavily damaged areas while in moderately damaged areas, the most common mosses were *Rhytidiadelphus triquetrus*, *Plagiochila asplenioides*, *Pleurozium schreberi*, *Hylocomium splendens* and *Sphagnum* spp. *Rhytidiadelphus triquetrus*, *Plagiomnium* spp., *Hylocomium splendens*, *Sphagnum* spp. and *Eurhynchium angustirete* were found in logged plots. The nomenclature follows the *Key-Book of Estonian Plants* (Leht, 1999).

The regeneration surveys were performed in two subsequent years (autumn 2004 and autumn 2005) in pits, on mounds and on 10 1 m^2 squares which were established on undamaged forest floor along the middle transect of each plot (Fig. 1). The species of each uprooted tree was recorded and its mound width and pit depth measured with a tape-measure. The perimeter points of pits and mounds and locations of seedlings were mapped using a surveyor's compass and electronic distance and height meter Vertex III (Haglof, Inc.) and areas of pits and mounds were calculated using the circle sector area formula to determine the density of seedlings.

The number of tree seedlings was recorded by species, and seedling height was measured. The height increment was calculated as the difference in height in successive surveys. Location (pit, mound or undamaged) and species were determined. Pre- and post-disturbance seedlings and sprouts were separated by a visual survey, and only data from seedlings established after the storm were used in statistical analyses (Tables 1 and 2). Seedling density was found by dividing the number of trees by the area of the microsite, the result being categorized into three density classes (I class <5 seedlings; II class <10 seedlings; III class ≥ 10 seedlings per m^2). The pre-disturbance regeneration comprised approximately 7% of all regeneration trees in moderately and heavily damaged areas in 2004. When only regeneration trees on intact forest floor were considered, the given proportion was 27%.

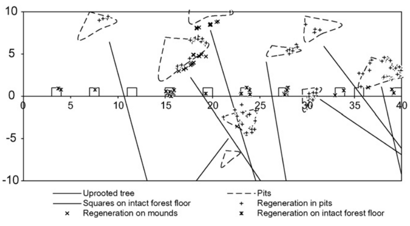

Fig. 1. An example of a study plot in a heavily damaged area. The uprooted trees, pits, intact forest floor squares and regeneration trees have been mapped using the *x*, *y* coordinate system.

Table 1
Status of tree recruitment in 2004 (numbers refer to individuals that survived to 2005, categorized by species)

	Pit		Mound		Intact		Harvested	
	Surviving	Dead	Surviving	Dead	Surviving	Dead	Surviving	Dead
Aspen	5	13	1	–	5	8	26	12
Birch	94	130	5	3	17	7	77	93
Spruce	26	15	27	2	33	2	6	–
Alder	65	135	–	–	6	2	–	–
Rowan	12	15	51	34	37	21	9	1

The data of trees in pit, mound and intact microareas comes from moderately and heavily damaged plots.

Kruskal–Wallis ANOVA was performed first to find the effect of disturbance severity and microsite on seedling density. The Mann–Whitney *U* test was then performed on seedling densities among microsites to test for pairwise species microsite preference.

The increment of recruitment trees was logarithmically transformed and nested ANOVA was used to determine the influence of study plot, soil type (gley or gleyed podzolic), storm year (2001 in Halliku Forest District and 2002 in Tudu Forest District), damage severity (heavily or moderately damaged), microsite (pit, mound or intact forest floor) and recruitment tree species (birch, spruce, black alder, aspen, rowan) on increment. One-way ANOVA was used to examine the influence of microsite, pooled seedling density classes on microsite and density classes of particular species being studied. The Tukey test was used to find differences within the factor groups.

Logistic regression was used to examine factors that influence the mortality of tree seedlings. The 2004 heights of seedlings that lived to 2005 and those that died by 2005 were compared. The probability of surviving was tested as a logistic function of tree height and the following characteristics: (i) recruitment tree species, (ii) microsite, (iii) damage severity, (iv) soil type, (v) year of storm, (vi) pooled seedling density on microsite and (vii) density of a particular species on microsite. Analyses were also performed with recruitment tree species separately.

The program Statistica 6 (StatSoft, Inc.) was used for data analysis.

3. Results

Species composition of seedlings differed in areas with different damage severity and among microsites (Table 3). The Shannon diversity was highest in areas with moderate damage, followed by heavily damaged areas. The least diversity and eveness were found in harvested plots, where birch strongly dominated (Fig. 2). Pits showed the highest diversity among microsites. Species were also more evenly distributed in pits.

The damage severity had significant influence on pooled total seedling density and densities of aspen, birch, spruce, alder and rowan (Kruskal–Wallis tests, $p < 0.001$ in all cases). The pooled total seedling density and density of aspen seedlings were higher in harvested plots than heavily damaged and moderately damaged plots. The density of birch was highest in harvested plots and lowest in moderately damaged plots. Spruce was least abundant in harvested areas. Rowan

Table 2
Mean tree heights (in cm) and standard errors (S.E.) of tree recruitment in 2004

	Pit		Mound		Intact		Harvested	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Aspen								
Surviving	115	33.05	40	–	86	13.36	61.7	4.98
Dead	22.3	7.55	–	-	80.6	13.9	55.4	10.54
Birch								
Surviving	21.3	2.08	32.8	11.9	39	8.26	28.4	2.53
Dead	9.71	0.6	8.33	3.33	45	20.35	18.4	1.66
Spruce								
Surviving	18.2	1.69	34.81	4.4	62	7.56	29.2	7.12
Dead	26.06	4.33	18	7	20	5	–	–
Alder								
Surviving	6.9	0.36	–	–	226.7	59.1	–	–
Dead	5.3	0.2	–	–	32.5	2.5	–	–
Rowan								
Surviving	85.6	12.73	72.3	6.16	116.9	13.56	76.7	17.02
Dead	39.9	8.17	70.5	9.45	46.7	15.45	10	–

The data on trees in pit, mound and intact microsites comes from moderately and heavily damaged plots.

Table 3
Shannon diversity (H') and evenness (E_h) of five recruitment tree species (based on seedling densities)

	H'	E_h
Damage severity		
Harvested	0.741404	0.53481
Heavy	1.1358	0.705712
Moderate	1.169148	0.726433
Microsite		
Pit	0.81853	0.508581
Intact	0.595424	0.369958
Mound	0.545539	0.393523

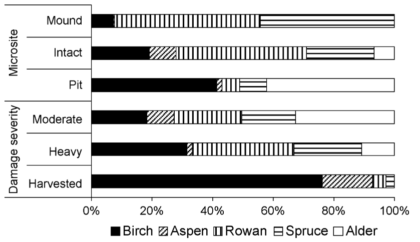

Fig. 2. Composition of seedlings (based on seedling density) in three different microsites (pit, mound, intact) and areas with different damage severity (heavy, moderate, harvested) in 2004.

densities were highest in heavily damaged areas and alder on moderately damaged areas (Fig. 3).

Microsite significantly affected pooled total densities (Kruskal–Wallis tests, $p = 0.0055$), as well as the densities of birch ($p < 0.001$) and alder ($p < 0.001$) (Fig. 4). The pooled total seedling density was the lowest on mounds compared to pits and intact area. Birch had highest seedling densities in pits. Alder was mostly in pits as well, only 8 trees being found on intact ground. Seedlings of other species did not show any preferences among microsites.

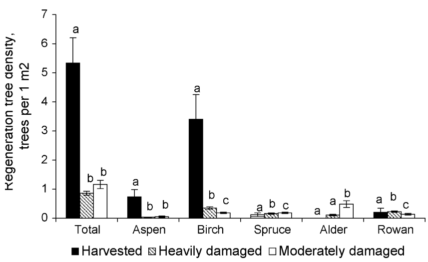

Fig. 3. Mean regeneration tree densities in areas with different damage severity in 2004. Standard errors of means are given as error bars. Letters above bars show the interspecific difference between areas with differential damage.

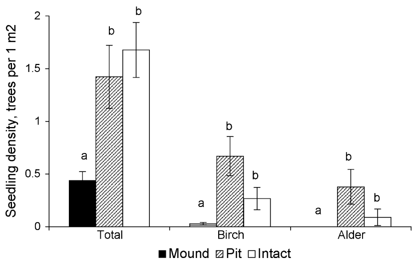

Fig. 4. Mean regeneration tree densities in three different microsites in moderately and heavily damaged areas in 2004. Standard errors of means are given as error bars. Letters above bars show the interspecific difference between microsites.

There was no significant influence of transect, damage severity, soil type or storm year on recruitment tree growth, but microsite and tree species showed significant influence (nested ANOVA, see Table 4**).** The incremental growth of birch and rowan was significantly greater with lower seedling density. Birch was most dense on mounds as against intact areas and pits, while rowan was least dense on intact areas (one-way ANOVA, see Table 5).

Survival of recruitment trees was influenced by seedling height and seedling species (logistic regression, $p < 0.001$ in both cases). Birches surviving to 2005 were significantly taller in 2004 than those that died by 2005 ($p < 0.001$). Surviving birches were also taller on gleyed podzolic soils ($p = 0.0187$) and on areas where birch seedling abundance was lower ($p = 0.0354$).

Survival of spruce did not depend on tree height, but the height differed among microsites ($p = 0.0024$). The tallest spruces were found on intact microsites and the shortest were in pits. Spruces were also taller in heavily damaged areas than those moderately damaged ($p = 0.0406$).

Surviving alders were taller in heavily damaged areas ($p < 0.001$), on gleyed soils ($p < 0.001$), with lower total seedling abundance ($p < 0.001$) and with lower alder seedling abundance ($p < 0.001$). Rowans and aspens surviving to 2005 were only significantly influenced by tree height ($p = 0.0081$ and $p < 0.001$ respectively). Those that were taller in 2004 had more chance of surviving to 2005.

Pit depth and mound thickness differed among uprooted species (Kruskal–Wallis tests, $p < 0.001$ in both cases). Uprooting of Norway spruce created the shallowest pits and thinnest root plates (Fig. 5). No significant differences in the numbers of seedlings on different uprooted tree species were found, although a slight trend for hardwood mounds to have more seedlings than spruce can be observed. In general, seedling abundance was relatively low on mounds.

4. Discussion

The recovery of a stand in the uncleared areas may be influenced by the very heterogeneous microtopography. The

Table 4
Summary of nested ANOVA on seedling increment

No. of analysis	Random effects	Sums of squares	Degree of freedom	Mean squares	Den. syn. error d.f.	Den. syn. error MS	F	p
I	Transect	29.219	7	4.17	15.05	2.5540	1.63	0.2004
	Microsite (Transect)	42.310	15	2.82	43.00	1.2249	2.30	0.0166
	Species (Transect × Microsite)	49.263	35	1.41	297.00	0.5598	2.51	0.0001
II	Severity	2.926	1	2.93	4.43	3.6917	0.79	0.4191
	Microsite (Severity)	18.759	4	4.69	21.33	2.4467	1.92	0.1445
	Species (Severity × Microsite)	68.747	17	4.04	332.00	0.5726	7.06	0.0001
III	Soil	0.070	1	0.07	4.40	4.1571	0.02	0.9026
	Microsite (Soil)	18.977	4	4.74	22.71	2.9205	1.62	0.2025
	Species (Soil × Microsite)	107.224	18	5.96	331.00	0.5704	10.44	0.0001
IV	Storm year	0.611	1	0.61	4.08	4.5568	0.13	0.7325
	Microsite (Storm year)	19.207	4	4.80	22.73	2.7383	1.75	0.1731
	Species (Storm year × Microsite)	90.313	18	5.02	331.00	0.5882	8.53	0.0001

pits, mounds and intact forest floor can vary greatly in nutrient level, soil moisture, light and temperature (Peterson et al., 1990; Bazzaz, 1996; DeLong et al., 1997; Carlton and Bazzaz, 1998; Clinton and Baker, 2000; Peterson and Pickett, 2000; Ulanova, 2000; Ruel and Pineau, 2002), which implies greater species diversity in uncleared areas, as confirmed in our study.

The harvested plots exhibit the highest degree of disturbance. Harvesting machines seriously damage the ground and forest vegetation after windthrow (Lüscher, 2002; Small and McCarthy, 2002) including advanced regeneration (Močalov and Lässig, 2002). When not damaged, advance regeneration can potentially dominate recovery of windthrow areas (Hytteborn and Packham, 1987; Dyer and Baird, 1997; Peterson, 2000; Ulanova, 2000; Drobyshev, 2001; Schönenberger, 2002; Wohlgemuth et al., 2002; Rammig et al., 2006). Thus harvesting is likely to alter species composition for many decades by increasing the representation of pioneer species such as aspen and birch in our study. This trend is also confirmed by several other studies (Schönenberger, 2002; Močalov et al., 2003).

The seedling densities were greater in harvested plots than in heavily and moderately damaged areas. Schönenberger (2002) and Wohlgemuth et al. (2002), who also compared uncleared and harvested plots, achieved similar results. Schönenberger (2002) suggested that fallen logs in uncleared areas may be an obstacle to seedling establishment during the first decades. Such negative effects could occur through influences on germination, establishment or growth. Surprisingly, there were no differences between moderately and heavily damaged stands in species diversity and seedling densities, increment growth and height. The amount of light reaching the ground should be considerably less in moderately damaged areas because of the remaining partial canopy, which should reduce the growth rates of regenerating seedlings (Harrington and Bluhm, 2001). One explanation of the apparent similarity between the two damage classes may be that the extremely large number of fallen trunks and coarse debris in heavily damaged areas provides shade (Ilisson et al., 2005a). If this is so, a faster growth rate is to be expected in heavily damaged areas when regeneration exceeds the height of the fallen trunks.

Crushed vegetation and eliminated moss carpet due to windthrow can efficiently contribute to the establishment of seeds (DeLong et al., 1997; Wohlgemuth et al., 2002). As pits are the areas in the forest floor where mineral soil is exposed, they provide good opportunities for the germination and establishment of small-seeded species like birch and alder in our study (see also Peterson et al., 1990; Bazzaz, 1996; Kuuluvainen and Juntunen, 1998; Peterson and Pickett, 2000; Ulanova, 2000), whereas spruce (intermediate-sized seeds) and rowan (large-seeded) showed indifference to microsite

Table 5
Summary of one-way ANOVA on seedling increment

Fixed factor	Sums of squares	Degree of freedom	Mean squares	F	p
Birch					
Microsite	3.3051	2	1.6525	3.785	0.0256
Density classes	4.5850	2	2.2925	5.391	0.0058
Rowan					
Microsite	22.7817	2	11.3908	16.789	0.0001
Density classes	11.5071	2	5.7536	4.8392	0.0099

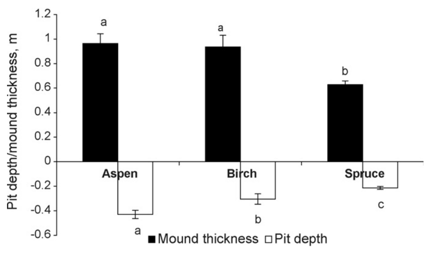

Fig. 5. Pit depth and mound thickness depending on the tree species of the uprooted tree. Letters above bars show the significant differences between species.

However, the environmental conditions of pits are quite unfavorable for seedlings. Clinton and Baker (2000) suggested that tree-fall pits have excessive soil moisture content and risk of seasonal flooding. During spring or after a large precipitation event, seedlings in pits can suffer because of overflow (Harrington and Bluhm, 2001). Lüscher (2002) reported that the water content also increases because of the lack of interception by canopy trees. At the same time, the temperatures increase near the soil surface. Thus pits can have very wet or very dry phases, depending on the weather conditions, a possible reason for the low density of some species in pits.

Survival of seedlings in tree-fall pits can be also problematic because of greater accumulation of litter and burial under soil slides falling from mounds during heavy rains (Bazzaz, 1996; Ulanova, 2000; Harrington and Bluhm, 2001). Peterson et al. (1990) point out that the pits accumulate litter differentially from part to part. For example, in our study the accumulation during the third year after the storm decreased in the middle and outer edge of pit, but the erosion from the mound increased. Harrington and Bluhm (2001) noted that every seedling not located near the periphery of the windthrow pit was buried sooner or later. The success of seedlings that germinate in pits may depend on individual growth rate, since taller trees may survive partial burial. Moreover, the competition within and between tree species is significant.

Norway spruce is one of the few natural tree species in Northern Europe that is able to establish itself in shade and grow into overstory. Spruce density certainly increased with decreasing disturbance severity. Although in our study they were smallest and lowest in density in pits compared to other microsites where birch and alder showed no marked difference, spruce seedlings had the lowest mortality figure of all species in pits. A reason for small seedlings and low densities of spruce in pits could be the later time of establishment because of difficult environmental conditions rather than the lower light availability in pits as suggested by Clinton and Baker (2000).

While the light availability and temperature are highest on mounds (Clinton and Baker, 2000), the regeneration densities were lowest there. This is probably due to soil instability and dryness (DeLong et al., 1997), although this is difficult to establish. In our study, spruce tree-fall mounds were significantly thinner than aspen and birch mounds, which may lead to more rapid erosion. However, seedling density on mounds was too low overall for significant results. In general, some time lapse is probably needed for mound collapse and successful seedling establishment on a more stable surface. The location above the forest floor on mounds might give seedlings a great advantage in ascending to the canopy (Bazzaz, 1996), but this potential microsite benefit has not yet been rigorously demonstrated.

Natural regeneration in uncleared areas is a long-term process (Hytteborn and Packham, 1987; Schönenberger, 2002) and future seedling establishment may increase as fallen logs decompose sufficiently to become good seedbeds (Hytteborn and Packham, 1985; Hofgaard, 1993; Grey and Spies, 1997; Cornett et al., 2001; Wohlgemuth et al., 2002). Observations by Wohlgemuth et al. (2002) suggest that fallen logs provide recruitment opportunities for *Picea abies* seedlings seven years after the storm. Because only 3–4 years have passed since the storm events in our study areas, there was no regeneration found on logs – the fourth microsite in our study – as yet. Future research in these areas, with such a great amount of dead wood, should determine whether logs play an important role as seedbeds. In that case, we expect that the importance of spruce regeneration in uncleared areas will increase over several decades, producing a mixed, uneven-aged stand.

Two other functions of storm-felled trees iare to protect seedlings against animal browsing (Long et al., 1998; Schönenberger, 2002; Krueger and Peterson, 2006; De Chantal and Granström, 2007) and possibly to alter nutrient dynamics. Some of the nutrients from the dead wood leaches into the forest soil (Hyvönen et al., 2000) and can be taken up by regenerating seedlings (Bormann and Likens, 1994; Krankina et al., 1999). Because the decomposition rate is found to be negatively correlated with size of dead wood (Harmon et al., 1986; Harmon and Sexton, 1996; Mackensen et al., 2003), uncleared areas with abundant dead wood may offer nutrient input from leaching for a longer period. Our intention is to examine the soil and dead wood nutrient content in the future to document this process.

5. Conclusions

The recovery of windthrow areas may be strongly influenced by the cumulative severity of natural and anthropogenic disturbances. This study has shown that extent of canopy destruction and logging activities influence regeneration patterns. Such findings agree with the predictions of recent conceptual models (Frelich, 2002; Roberts, 2004) that high severity is likely to produce major changes in species composition. Post-windthrow harvesting increases disturbance severity, and the results reported here demonstrate how small-seeded pioneer species benefit from soil disruption and open areas by rapid establishment, resulting in less seedling species diversity than unharvested windthrow areas.

An important influence on regeneration in uncleared areas is the physical and environmental heterogeneity created by pit and mound microrelief and the large amount of dead wood. While pits are found to be the most suitable establishment locations for small-seeded tree species like birch and alder, the seedling survival is quite poor because of flooding and erosion. The competition between and within species plays an important role. Seed establishment on mounds is less frequent than on other microsites, perhaps because of the instability of the substrate. Establishment is more likely on mounds of uprooted hardwood species that have a thicker root plate than spruce. The variation in species preferences and survival opportunity in different microsites means that the heterogeneity of unharvested post-disturbance stand structure contributes to greater species diversity. Large-seeded and shade tolerant species do not show a particular preference for microsites for germination and growth. The findings of this study do not support the suggestion by Schönenberger (2002) that fallen logs left in situ are detrimental to regeneration by mature-forest species such as spruce.

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References

Bazzaz, F.A., 1996. Plants in Changing Environments. Linking Physiological, Population, and Community Ecology. Cambridge University Press, Cambridge, England, pp. 256–263.

Beschta, R.L., Rhodes, J.J., Kauffman, J.B., Gresswell, R.E., Minshall, G.W., Karr, J.R., Perry, D.A., Hauer, F.R., Frissell, C.A., 2004. Postfire management on forested public lands of the western United States. Conserv. Biol. 18, 957–967.

Bormann, F.H., Likens, G.E., 1994. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, Inc., p. 253.

Carlton, G.C., Bazzaz, F.A., 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. Ecology 79, 1305–1319.

Clinton, B.D., Baker, C.R., 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. Forest Ecol. Manage. 126, 51–60.

Cornett, M.W., Puettmann, K.J., Frelich, L.E., Reich, P.B., 2001. Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* forests of Northern Minnesota. Rest. Ecol. 9, 386–396.

De Chantal, M., Granström, A., 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. Forest Ecol. Manage. 250, 3–8.

De Chantal, M., Leihonen, K., Kuuluvainen, T., Cescatti, A., 2003. Early response of *Pinus sylvestris* and *Picea abies* seedlings to an experimental canopy gap in a boreal spruce forest. Forest Ecol. Manage. 176, 321–336.

DeLong, H.B., Lieffers, V.J., Blenis, P.V., 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixed woods. Can. J. Forest Res. 27, 1452–1457.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science Express, 5 January 2006.

Drobyshev, I.V., 2001. Effect of natural disturbances on the abundance of Norway spruce (*Picea abies* (L.) Karst.) regeneration in nemoral forests of the (??) southern boreal zone. Forest Ecol. Manage. 140, 151–161.

Dyer, J.M., Baird, P.R., 1997. Wind disturbance in remnant forest stands along the prairie-forest ecotone, Minnesota, USA. Plant Ecol. 129, 121–134.

Frelich, L.E., 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge University Press, Cambridge.

Greenberg, C.H., McNab, W.H., 1998. Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. Forest Ecol. Manage. 104, 179–191.

Grey, A.N., Spies, T.A., 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78, 2458–2473.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.

Harmon, M.E., Sexton, J., 1996. Guidelines for Measurements of Woody Detritus in Forest Ecosystems. U.S. Long Term Ecological Research (LTER) Network. N. M. Publ., Allbuquerque, p. 20.

Harrington, T.B., Bluhm, A.A., 2001. Tree regeneration responses to microsit characteristics following a severe tornado in the Georgia, Piedmnont, USA Forest Ecol. Manage. 140, 265–275.

Hofgaard, A., 1993. Structure and regeneration patterns in a virgin *Picea Abie* forest in Northern Sweden. J. Veg. Sci. 4, 601–608.

Hytteborn, H., Packham, J.R., 1985. Left to nature: forest structure an regeneration in Fiby Urskog, Central Sweden. Arboric. J. 9, 1–11.

Hytteborn, H., Packham, J., 1987. Decay rate of *Picea abies* logs and the storn gap theory: a re-examination of Sernander plot III, Fiby Urskog, Centra Sweden. Arboric. J. 11, 299–311.

Hyvönen, R., Olsson, B.A., Lundkvist, H., Staaf, H., 2000. Decomposition an nutrient release from *Picea abies* (l.) Karst. and *Pinus sylvestris* L. logging residues. Forest Ecol. Manage. 126, 97–112.

Ilisson, T., Metslaid, M., Vodde, F., Jõgiste, K., Kurm, M., 2005a. Storn disturbance in forest ecosystems in Estonia. Scand. J. Forest Res. 20 (Suppl 20), 88–93.

Ilisson, T., Metslaid, M., Vodde, F., Jõgiste, K., Kurm, M., 2006. Vascular plan response to windthrow severity in Norway spruce-dominated *Myrtillus* sit type forests in Estonia. Ecoscience 13 (2), 193–202.

Karr, J.R., Rhodes, J.J., Minshall, G.W., Hauer, F.R., Beschta, R.L., Frissell C.A., Perry, D.A., 2004. The effects of postfire salvage logging on aquati ecosystems in the American West. BioScience 54, 1029–1033.

Krankina, O.N., Harmon, M.E., Griazkin, A.V., 1999. Nutrient stores an dynamics of woody detritus in a boreal forest: modeling potential implica tions at the stand level. Can. J. Forest Res. 29, 20–32.

Krueger, L.M., Peterson, C.J., 2006. Effects of white-tailed deer on *Tsug canadensis* regeneration: evidence of microsites as refugia from browsing American Midland Naturalist 156 (2), 353–362.

Kuuluvainen, T., Juntunen, P., 1998. Seedling establishment in relation t microhabitat variation in a windthrow gap in a boreal *Pinus sylvestri* forest. J. Veg. Sci. 9, 551–562.

Köster, K., 2005. Puidu lagunemise dünaamika Halliku ja Tudu tormialade (Coarse woody debris decay dynamics in Tudu and Halliku windthrow areas). Magistritöö. Eesti Põllumajandusülikool, Metsandus-ja maaehitu sinstituut. 50 pp. (in Estonian with English abstract).

Leht, M. (Ed.), 1999. Eesti taimede määraja (Key-Book of Estonian Plants) EPMÜ ZBI, Eesti Loodusfoto, Tartu, p. 447.

Lindemann, J.D., Baker, W.L., 2001. Attributes of blowdown patches from severe wind event in the Southern Rocky Mountains, USA. Landsc. Ecol 16, 313–325.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F. Schmiegelow, F.A., Perry, D., 2004. Salvage harvesting policies afte natural disturbance. Science 303, 1303.

Long, Z.T., Carson, W.P., Peterson, C.J., 1998. Can disturbance create refugi for herbivores: An example with hemlock regeneration on treefall mounds J. Torrey Bot. Soc. 125, 165–168.

Lõhmus, E., 2004. Eesti metsakasvukohatüübid (Estonian Forest Site Types) Eesti Loodusfoto 80.

Lässig, R., Močalov, S.A., 2000. Frequency and characteristics of severe storm in the Urals and their influence on the development, structure and manage ment of the boreal forests. Forest Ecol. Manage. 135, 179–194.

Lüscher, P., 2002. Humus dynamics and changes in rooting patterns in wind throw areas. For. Snow. Landsc. Res. 77, 49–60.

Mackensen, J., Bauhus, J., Webber, E., 2003. Decomposition rates of coars woody debris—A review with particular emphasis on Australian tre species. Aust. J. Bot. 51, 27–37.

McAlister, S.D., Palmer, M.W., Arevalo, J.R., DeCoster, J.K., 2000. Specie composition on tipup mounds and pits created by catastrophic windthrow i a Minnesota forest. In: Proceedings IAVS Symposium. pp. 104–107.

Močalov, A.S., Lässig, R., 2002. Development of two boreal forests after large scale windthrow in the Central Urals. For. Snow. Landsc. Res. 77, 171–186

Močalov, S.A., Lässig, R., Moiseev, P.A., Nechaeva, V.A., Fedorenko, S.I. Michailov, Y.E., Syusko, A.Y., Benkov, A.V., Lischke, H., Zoteeva, E.A. 2003. Consequences of large-scale windthrow on the regeneration an diversity of two boreal forests in the Central Urals. In: Ruck, B., Kott meier, C., Mattheck, C., Quine, C., Wilhelm, G. (Eds.), Wind Effect o Trees. Proceedings of the International Conference, University of Karls ruhe, Germany, 16–18 September, p. 87.

Peterson, C.J., Carson, W.P., McCarthy, B.C., Pickett, S.T.A., 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58, 39–46.

Peterson, C.J., 2000. Damage and recovery of tree species after two different tornadoes in the same old growth forest: comparison of infrequent wind disturbances. Forest Ecol. Manage. 135, 237–252.

Peterson, C.J., Pickett, S.T.A., 2000. Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. Oikos 90, 489–500.

Rammig, A., Fahse, L., Bugmann, H., Bebi, P., 2006. Forest regeneration after disturbance: A modelling study for the Swiss Alps. Forest Ecol. Manage. 222, 123–136.

Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. Can. J. Bot. 82, 1273–1283.

Ruel, J.C., Pineau, M., 2002. Windthrow as an important process for white spruce regeneration. Forestry Chronicle 78, 732–738.

Schönenberger, W., 2002. Post windthrow stand regeneration in Swiss mountain forests: the first ten years after the 1990 storm Vivian. For. Snow. Landsc. Res. 77, 61–80.

Small, C.J., McCarthy, B.C., 2002. Effects of simulated post-harvest light availability and soil compaction on deciduous forest herbs. Can. J. For. Res. 32, 1753–1762.

Ulanova, N.G., 2000. The effects of windthrow on forest at different spatial scales: a review. Forest Ecol. Manage. 135, 155–167.

Wohlgemuth, T., Kull, P., Wüthrich, H., 2002. Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivian 1990. For. Snow. Landsc. Res. 77, 17–48.

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NUTRIENTS IN COARSE WOODY DEBRIS AND FOREST REGENERATION IN WINDTHROW AREAS

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Abstract

Köster, K., Ilisson, T., Jõgiste, K. Nutrients in coarse woody debris and forest regeneration in windthrow areas. – Miškininkystė, 2007, Nr. 1 (61), Supplement No 1, 14–19.

This study examined changes in coarse woody debris (CWD) nutrient concentrations and in soil nutrient content in two windthrow areas in eastern Estonia, which experienced storms on summer of 2001 and 2002. Norway spruce (*Picea abies* L. Karst.) was the dominant tree species in these areas. We also examined, how does the disturbance severity and soil nutrient concentration influence recovery of areas with different damage severity. 3–4 years after disturbance there were no changes in nutrient concentration of CWD in windthrow areas. The concentration of three main nutrients (N, P, K) stayed stable (no increase inside the material and no leaching out to the soil). The regeneration seedling density was highest in harvested plots.
Keywords: dead wood, Norway Spruce stands, regeneration, soil, nutrients, windthrow.

Introduction

Dead wood is recognised as important component of the forest ecosystems, linked to biodiversity and ecosystem processes (Harmon et al., 1986; Esseen et al., 1992; Angelstam, 1998; Karjalainen and Kuuluvainen, 2002), but the role of coarse woody debris (CWD) in the nutrient dynamics of forests is far less clear.

Natural disturbances have major role in dynamics of forest ecosystems. The severity of disturbance determines the share of species with different climatic preferences in forest ecosystem. Relatively small disturbances may result in small changes in stand composition, while extensive dieback induced by catastrophic natural disturbances (fires, windthrows, massive insect outbreaks, etc.) is followed by the establishment of pioneer plant communities – both regeneration and ground vegetation (Gromtsev, 2002).

The role of CWD in nutrient cycling of wind damaged forests and regeneration development in areas with different canopy damage extent are examined in this study. The aim is to find out changes in CWD nutrient concentrations and in soil nutrient content and also examine how does the disturbance severity and soil nutrient content influence recovery. We hypothesize that because of leaching from CWD, nutrient content is higher in damaged areas where dead wood is left untouched. Secondly we expect the positive influence of higher nitrogen, phosphorus, potassium (N, P, K) concentrations to regeneration density.

Material and methods

The study areas were situated in the east of Estonia, in Tudu Forest district (59°11' N 26°52' E) (approximately 6 hectare) and Halliku Forest District (58°43' N 26°55' E) (approximately 10 hectare), which experienced storms on 16 July 2001 and 5 July 2002, respectively. Areas were situated in hemiboreal vegetation zone (Ahti *et al*., 1968). Norway spruce (*Picea abies* L. Karst.) was the dominant tree species in the areas. European aspen (*Populus tremula* L.), black alder (*Alnus glutinosa* (L.) J. Gaertn.), silver birch (*Betula pendula* Roth.), downy birch (*Betula pubescens* Ehrh.) and rowan (*Sorbus aucuparia* L.) were some of the secondary tree species (Table 1). The study areas include stands on Eutric Gleysols and Calcaric Cambisols (FAO, ISSS, ISRIC, 1998 and Reintam *et al.,* 2001), *Filipendula* and *Myrtillus* forest site types (Lõhmus, 1984) being most commonly represented (Ilisson *et al.,* 2005).

Ten permanent sample plots (20×40 m) were established on storm-damaged areas in Tudu (2002) and eight in Halliku (2003). Four types of plots were set up: (i) with total canopy destruction (all of the trees damaged by storm; four plots), (ii) partial canopy destruction (approximately half of the trees damaged; five plots), (iii) logged after canopy destruction (trees storm felled and then logged; five plots) and (iiii) control areas (with no damage; four plots). The stand ages were in range from 110 to 160 years (Table 1).

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 removed timber for harvested 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.) (Ilisson et al., 2005)*

Location	Damage type	Site type	Composition	Year of birth	Volume (m3/ha)
Tudu	Totally	*Myrtillus*	45Sp 43As 12Bi	1865	616
Tudu	Control	*Myrtillus*	73Sp 11As 7Al 5As	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	-	238
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	-	303
Halliku	Harvested	*Myrtillus*	44As 37Bi 11Al 5As	-	300
Halliku	Harvested	*Myrtillus*	40Bi 30Sp 29As 1Ma	-	261
Halliku	Partly	*Filipendula*	53Sp 30Al 13Bi 2Ac	1873	138/217
Halliku	Control	*Filipendula*	57Al 28As 9Ac 3Bi 3Sp	1958	292
Halliku	Partly	*Myrtillus*	76Sp 16As 6Bi 1As	1893	225/105
Halliku	Partly	*Filipendula*	82Al 11Sp 6As	1898	277/264
Halliku	Totally	*Myrtillus*	82Sp 17Bi 1As	1893	230.5543

The regeneration surveys were made in two subsequent years (autumn 2004 and autumn 2005) in pits, on mounds and on 10 undamaged forest floor squares inside each study plot (located on 40 m transect). A detailed description of regeneration measurement methods has been published earlier (Ilisson *et al.,* 2007).

4 soil samples were taken from each sample plot. Soil samples were linked with those 10 undamaged forest floor squares and taken randomly from the other side of the transect. Samples were taken from depth 5-15 cm and analysed in laboratory to find N, P, K content of the soil and pH_{KCl}.

For wood nutrient concentration measurements sample trees were selected from permanent sample plots. In total we analysed 58 sample logs and snags. The sample snags (standing dead) or logs (dead lying or leaning) were randomly selected from Norway spruce and birch. From sample trees (represented by logs and snags >10 cm in diameter and > 1.3 m in length) sample disks (2–5 cm thick) were taken from three cross sections of the tree, 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. Wood probes (ca 20 g) were taken from each disk, weighted and air-dried in paper bags to stop decomposition. In total 134 wood samples of two tree species (spruce and birch) were taken from differently damaged areas (samples from CWD) and from control areas (samples from living trees). N, P, K content of the wood was analysed to determine the changes in wood nutrient content.

The main statistical analysis was carried out with the SAS procedure 'Mixed' (Release 8.2). This procedure realises the general linear mixed model analysis, which in the present case enabled us to test possible changes in CWD and in soil nutrient content, also whether, and how, the nutrient content in soil influences the regeneration development of the stand. Kruskal-Wallis ANOVA by Ranks and program Statistica 6 was used to investigate regeneration densities in areas with different damage severity. The Spearman rank-order correlation was used to investigate influence of different nutrients (N, P, K) to different tree species.

Results and discussion

The results of this study revealed, that 3–4 years after disturbance there was no statistically significant change in CWD nutrient concentration. Angiosperm wood generally has higher elemental concentration than gymnosperm wood (Harmon et al., 1986) and our study showed that nutrient content in birch wood was higher than in spruce wood (Figures 1 and 2). But damage severity and snag/log position had no significant influence on wood nutrient concentration (Figures 1 and 2).

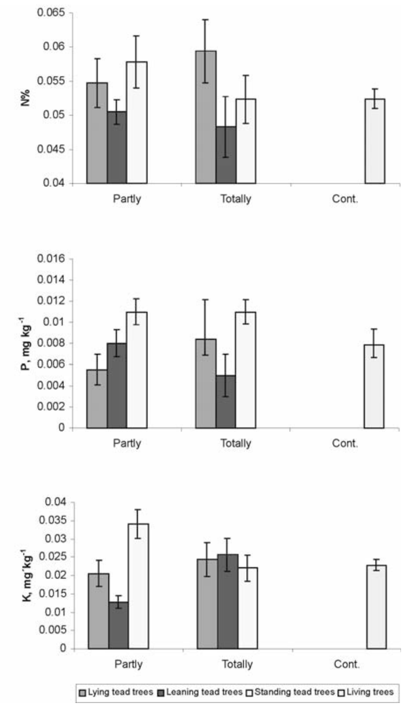

Fig. 1. Spruce wood nutrient concentration in stands with different damage severity. Where Partly means partly damaged area, Totally means totally damaged area and Cont. means control area with living trees

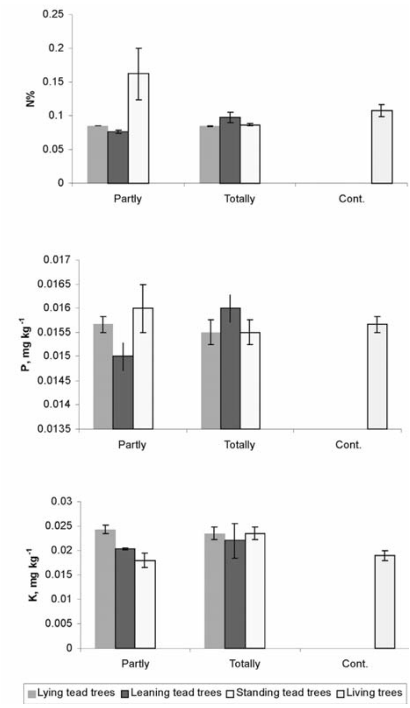

Fig. 2. Birch wood nutrient concentration in stands with different damage severity. Where Partly means partly damaged area, Totally means totally damaged area and Cont. means control area with living trees

Therefore 3–4 years after disturbance there were no changes in nutrient concentration of CWD in windthrow areas. The concentration of three main nutrients (N, P, K) stayed stable. In partly damaged areas and in totally damaged areas the lying and leaning dead trees showed changes in nutrient concentrations (decrease, increase) but no trends were become visible. Standing snags on these areas showed almost no changes in nutrient concentrations when compared with living trees. Only element that showed increase was K, but this also didn't come statistically significant. Here the reason can be that K is recognized as highly mobile element and it concentration may increase at the beginning of decay processes.

Also the N, P, K content of soil profile showed no significant difference between areas with different damage severity inside the site type, but it differed between *Myrtillus* and *Filipendula* site types (Figure 3). The only exception was the concentration of N, P and K in *Filipendula* site type on partly damaged areas. One explanation here can be, that the sample plot from where the soil samples were taken is not pure *Filipendula* site type but transition to other site type (transition to *Myrtillus* site type).

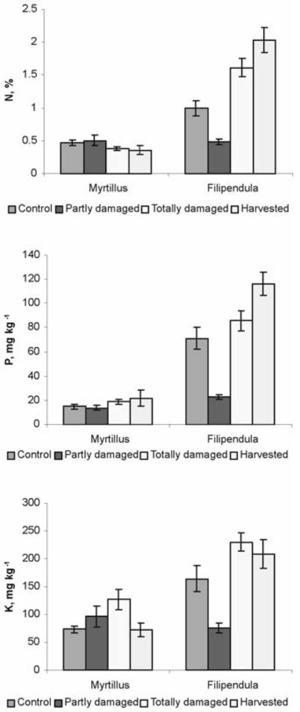

Fig. 3. *Soil nutrient concentration in Myrtillus and Filipendula stands with different damage severity*

The higher nutrient content in *Filipendula* stands is explainable with better soil nutrient potential developed during soil formation. A pulse of dead wood is acting as temporary nutrient storage, but it often takes several decades of decay before dead wood starts to act as a nutrient source (Krankina et al., 1999; Laiho and Prescott, 2004).

From the point of view of stand development in the future the site fertility is important. More fertile sites (*Filipendula* site type in our case) have a greater potential of natural regeneration in totally damaged and especially harvested plots (Figure 4), where greater amount of N, P and K in the soil had positive influence on total density and density of birch and Norway spruce.

Studied nutrients did not influence regeneration density in partly damaged areas (did not become statistically significant). We can conclude, that some other environmental factor than nutrient content is co-influencing the regeneration establishment rate few years after the storm. Smaller light level may be the inhibiting factor (Harrington and Bluhm, 2001) in partly damaged areas.

The damage severity had major role in regeneration patterns of storm-damaged areas. Different species showed certain stand preferences. The regeneration seedling density was highest in harvested plots, so were the densities of studied pioneer species – aspen and birch (Figure 5). The rapid colonization of harvested areas by pioneer species is recorded by many authors (Močalov and Lässig, 2002; Schönenberger, 2002). Here also the reason can be that during harvesting operations (cutting and transportation) the mineral soil layer will be exposed and pioneer species can easily regenerate. Quite even-aged mixed stand can be expected in the future on these areas. On damaged areas aspen seedlings were almost absent. Some of birch seedlings were found on totally damaged areas, but almost no seedlings on partly damaged areas. Partly damaged areas are still to shade for these pioneer species. Spruce was represented in all areas, but the seedling density was really low (Figure 5). Alder was absent on harvested areas, while on partly damaged areas it was represented (Figure 5).

Age structure of the developing stand in partly and totally damaged areas had greater variation compared to harvested areas due

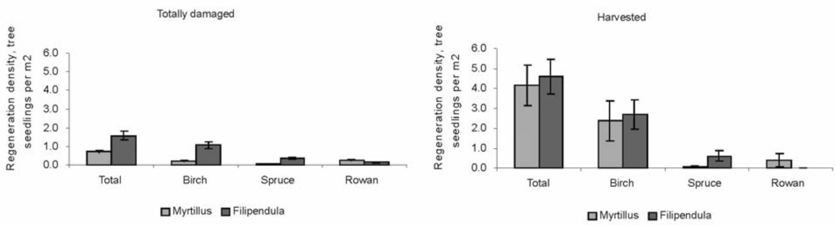

Fig. 4. *Regeneration density in Myrtillus and Filipendula stands with different damage severity*

to surviving old trees, advanced regeneration and gradual regeneration. However, the long-term dynamics of N, P, K leaching from dead organic matter will influence regeneration pattern (Bormann and Likens, 1994; Krankina et al., 1999). A certain delay within dead wood nutrient release may influence regeneration in nutrient poor soils, causing delayed regeneration impulse and uneven age structure. Dead wood also is expected to offer effective seed establishment patches in the future (Hytteborn and Packham, 1985; Grey and Spies, 1997; Stevens, 1997) increasing the future age and species diversity.

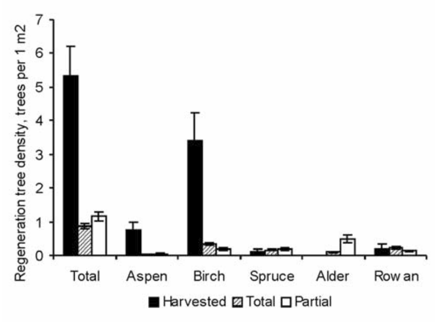

Fig. 5. *Mean densities of tree seedlings in areas with different damage severity*

Conclusion

The results of this study revealed, that 3–4 years after disturbance there was no statistically significant change in CWD nutrient concentration. The concentration of three main nutrients (N, P, K) stayed stable (no increase inside the material and no leaching out to the soil). Also the N, P, K content of soil profile showed no significant difference between areas which once more confirms that nutrients will be not released at early stage of decomposition of tree. After disturbance the regeneration density was highest in harvested plots. Species that were regenerating were the typical pioneer tree species – aspen and birch.

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in the northwestern Europe. Ann. Bot. Fen. 5: 169–211.

Angelstam, P.K. 1998: Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. J. Veg. Sci. 9: 593–602.

Bormann, F.H., Likens, G.E. 1994. Pattern and Process in a Forested Ecosystem. Springer-Verlag New York, Inc., 253 p.

Esseen, P-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1992. Boreal forests- the focal habitats of Fennoscandia. – In: Hansson, L. (ed.), Ecological principles of nature conservation. Applications in temperate and boreal environments. Elsevier Science Publishers, London. p. 252–325.

FAO, ISSS, ISRIC, 1998. World reference base for soil resources. World Soil Resources Rep. 84, Rome.

Grey, A.N., Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78(8): 2458–2473.

Gromtsev, A. 2002. Natural Disturbance Dynamics in the Boreal Forests of European Russia: a Review. Sillva Fenn. 36(1): 41–55.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133–302.

Harrington, T.B., Bluhm, A.A. 2001. Tree regeneration responses to microsite characteristics following a severe tornado in the Georgia, Piedmnont, USA. For. Ecol. Manage. 140: 265–275.

Hytteborn, H., Packham, J.R. 1985. Left to nature: forest structure and regeneration in Fiby Urskog, Central Sweden. Arboric. J. 9: 1–11.Ilisson, T., Metslaid, M., Vodde, F., Jõgiste, K. and Kurm, M. 2005. Storm disturbance in forest ecosystems in Estonia. Scan. J. For. Res. 20 (Suppl 6): 88–93.

Ilisson, T., Metslaid, M., Vodde, F., Jõgiste, K. and Kurm, M. 2005. Storm disturbance in forest ecosystems in Estonia. Scan. J. For. Res. 20 (Suppl 6): 88–93.

Ilisson, T., Köster, K., Vodde, F., Jõgiste, K. 2007. Regeneration in storm damaged forests in Estonia. For. Ecol. Manage. (Article in Press).

Karjalainen, L. & Kuuluvainen 2002. Amount and diversity of coarse woody debris within a boreal forest landscape dominated by Pinus sylvestris in Vienansalo wilderness, eastern Fennoscandia. Silva Fenn. 36(1): 147–167.

Krankina, O.N., Harmon, M.E., Griazkin, A.V. 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. Can. J. For. Res. 29: 20–32.

Laiho, R. and Prescott, C.E. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can. J. For. Res. 34: 763–777.

Lõhmus, E. 1984. Eesti metsakasvukohatüübid. (Estonian forest site types). Tallinn: ENSV ATK IJV. (In Estonian).

Močalov, A.S., Lässig, R. 2002. Development of two boreal forests after large-scale windthrow in the Central Urals. For. Snow. Landsc. Res. 77, 1/2: 171–186.

Reintam, L., Rooma, I. and Kull, A. 2001. Map of soil vulnerability and degradation in Estonia. In: D.E. Stott, R.H. Mohtar and G.C. Steinhardt, Editors, Sustaining the Global Farm. Selected papers from the 10th International Soil Conservation Organization Meeting held May 24–29, 1999, Purdue University, USDA-ARS NSERL p. 1068–1074.

Schönenberger, W. 2002. Post winthrow stand regeneration in Swiss mountain forests: the first ten years after the 1990 storm Vivian. For. Snow. Landsc. Res. 77, 1/2: 61–80.

Stevens, V. 1997. The ecological role of coarse woody debris: an overview of the ecological importance of CWD in B.C. forests. Res. Br., B.C. Min. For. Victoria, B.C. Work. Pap. 30/1997.

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Citizenship:	Estonian
Date of birth:	22.10.1979
Address:	Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia
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Martial status:	Married

Education:

2004-2008	Post-graduate Studies, Forest Management, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences
2003-2005	Master Studies in Forest Management, Faculty of Forestry, Estonian Agricultural University
2003-2004	MSc programme "Sustainable forestry around the Southern Baltic Sea region", Swedish University of Agricultural Sciences, Alnarp
1999-2003	Bachelor Studies in Forest Management, Faculty of Forestry, Estonian Agricultural University
1995-1998	Tõrva Gymnasium
1986-1995	Riidaja Primary School

Professional experience:

Since 2004	Estonian University of Life Sciences, Institute of Forestry and Rural Engineering; senior laboratory assistant (1.00)

Academic degrees

2005	M. Sc. in forest management for the thesis "Coarse woody debris decaying dynamics in Halliku and Tudu windthrow areas." (Estonian Agricultural University)

Projects

2009	“Economical and ecological estimation of forest windthrows and fires” (Environmental Investment Centre). Chief perfomer.
2008	TF project SF0170014s08: “The effect of changing climate on forest disturbance regimes in temperate and boreal zone”. Investigator.
2003-2008	“Economical and ecological estimation of forest windthrows and fires” (Environmental Investment Centre). Principal perfomer.
2005-2008	ESF grant No. 6087: „Animal-caused disturbances and their consequences in forest ecosystems“. Principal perfomer
2003-2007	TF project SF0432486s03: “Impact of natural disturbances and anthropogenic factors to dynamics and diversity of forest ecosystems”. Investigator.
2003-2007	“Natural disturbance dynamics analysis for forest ecosystem management” (Nordic Council of Ministers, Nordic Forest Research Co-operation Committee). Investigator.

Research interests

Research work is focused on dead wood (coarse woody debris) decay dynamics on windthrow areas

Knowledge of foreign languages

English, Russian, German

CURRICULUM VITAE

Eesnimi:	Kajar
Perekonnanimi:	Köster
Kodakondsus:	Eesti
Sünniaeg:	22.10.1979
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Haridus

2005	Eesti Maaülikool, Metsandus- ja maaehitusinstituut, metsanduse õppekava, doktoriõpe
2003-2005	Eesti Põllumajandusülikool, Metsandusteaduskond, metsamajandus, magistriõpe
2003-2004	Rootsi Põllumajandusteaduste Ülikool, magistriõpe
1999-2003	Eesti Põllumajandusülikool, Metsandusteaduskond, metsamajandus, bakalaureuseõpe
1995-1998	Tõrva Gümnaasium
1986-1995	Riidaja Põhikool

Teenistuskäik

Alates 2004	Eesti Maaülikool, Metsandus- ja Maaehitusinstituut, vanem laborant (1.00)

Akadeemilised kraadid

2005	Eesti Põllumajandusülikool, metsateaduste magister metsakasvatuse erialal, magistritöö "Puidu lagunemise dünaamika Halliku ja Tudu tormialadel"

Projektid

2009	"Tormikahjustuste ja metsapõlengute majanduslik ja ökoloogiline hindamine Eesti metsades" (SA Keskkonnainvesteeringute Keskus), vastutav täitja
2008	Sihtfinantseeritav teema SF0170014s08: "Muutuvate kliimatingimuste mõju boreaalse ja parasvöötme metsade häiringurežiimile", täitja

2003-2008	“Tormikahjustuste ja metsapõlengute majanduslik ja ökoloogiline hindamine Eesti metsades” (SA Keskkonnainvesteeringute Keskus), täitja
2005-2008	Eesti teadusfond, grant 6087: „Loomsed häiringud ja nende tagajärjed metsaökosüsteemides”, täitja
2003-2007	Sihtfinantseeritav teema SF0432486s03: “Looduslike häiringute ja inimtegevuse mõju metsaökosüsteemide dünaamikale ja mitmekesisusele”, täitja
2003-2007	“Häiringute analüüs metsaökosüsteemide majandamises” (Põhjamaade Ministrite Nõukogu, Põhjamaade Metsanduslik Uurimiskomitee), täitja

Teadustöö põhisuunad
Teadustöö on keskendunud puidu lagunemise dünaamikale tormialadel

Võõrkeelte oskus
Inglise, vene, saksa

LIST OF PUBLICATIONS

1.1. Publications indexed in the ISI Web of Science database:

Köster, K., Voolma, K., Jõgiste, K., Metslaid, M., Laarmann, D. 2009. Assessment of tree mortality after windthrow using photo-derived data. Annales Botanici Fennici 46, xx-xx (In print)

Köster, K., Ilisson, T., Tukia, H., Jõgiste, K., Möls, T. 2009. Rapid effects after forest disturbance in decomposition of trees in two windthrown areas in east Estonia. Baltic Forestry X, xx-xx (In print)

Ilisson, T., **Köster, K.,** Vodde, F., Jõgiste K. 2007. Regeneration development 4-5 years after a storm in Norway spruce dominated forests, Estonia. Forest Ecology and Management, 250, 17 - 24.

Köster, K., Jõgiste, K., Tukia, H., Niklasson, M., Möls, T. 2005. Variation and ecological characteristics of the coarse woody debris in Lahemaa and Karula National Parks, Estonia. Scandinavian Journal of Forest Research 20, 102-111.

Köster, K., Seedre, M., Tukia, H., Niklasson, M., Jõgiste, K. 2004. Nature conservation and dead wood in forest ecosystem. Transactions of the Faculty of Forestry, Estonian Agricultural University. 37, 13-16.

1.2. Papers in Estonian and in other peer-reviewed research journals with a local editorial board:

Köster, K., Kangur, A., Hari, P., Jõgiste, K. 2008. Test in Estonia at the southern border of the boreal zone. Hari, P.; Kulmala, L. (Toim.). Boreal forest and climate change (468 - 471).Springer

Köster, K., Ilisson, T., Jõgiste, K. 2007. Nutrients in coarse woody debris and forest regeneration in windthrow areas. Miškininkyste 1 (61), 13-18.

Köster, K., Seedre, M., Jõgiste, K., Tukia, H. 2003. The Quantitative Measurements of Coarse Woody Debris in Lahemaa and Karula National Parks in Estonia. Transactions of the Faculty of Forestry, Estonian Agricultural University. 36: 55-70.

Seedre, M., **Köster, K.,** Jõgiste, K. 2002. Metsaökosüsteemi looduslikkuse taastamine ja vastava katseala iseloomustus Lahemaa Rahvuspargis. Metsandusteaduskonna magistrantide ja doktorantide teaduslike tööde kogumik, EPMÜ Metsandusteaduskonna toimetised 35, 85-91.

1.3. Abstracts

Köster, K., Vodde, F., Jõgiste, K., Ilisson, T. 2008. The regeneration development in storm damaged areas with different damage severity. *In: Abstracts of conference on Feasibility of Silviculture for Complex Stand Structures. Designing Stand Structures for Sustainability and Multiple objectives: 6th Workshop of Uneven-aged Silviculture IUFRO 1.05 group, Shizuoka, 24-27 Oct, 2008, 148.*

Metslaid, M., **Köster, K.,** Jõgiste K. 2008. Stand structure and regenereation of Norway spruce forests in Estonia. *In: Abstracts of conference on Feasibility of Silviculture for Complex Stand Structures. Designing Stand Structures for Sustainability and Multiple objectives: 6th Workshop of Uneven-aged Silviculture IUFRO 1.05 group, Shizuoka, 24-27 Oct, 2008, 80.*

Köster, K., Metslaid, M., Jõgiste, K. and Ilisson, T. 2007. Species influence to the mechanism of wind damage in mixed stands. *In: Schedule and Abstracts for Oral and Poster Presenters. International Conference on Wind and Trees. IUFRO 8.01.11 : International Conference on Wind and Trees, Vancouver, British Columbia, Canada, August 5-9, 2007. Vancouver, British Columbia, Canada:, 2007. 83.*

Köster, K., Ilisson, T., Jõgiste, K. 2006. The regeneration development in storm damaged areas with different damage severity and nutrient (NPK) content in soil. *In: Abstracts of the Conference on Natural disturbance-based silviculture: Managing for complexity. IUFRO 1.05 Uneven-aged Silviculture Research Group: Natural disturbance-based silviculture: Managing for complexity, Rouyn-Noranda, QC, Canada, May 14 – 18, 2006. Rouyn-Noranda (Quebec, Canada):, 2006, 210 - 212.*

APPROBATION

International conferences and meetings

29.09.2005. Ilisson, T., **Köster, K.,**. Vodde, F., Jõgiste, K. "Regeneration in storm damaged forests in Estonia". In International Workshop on the scale of natural disturbances from tree to stand. 28-30 September 2005. Palanga, Lithuania.

29.09.2005. **Köster, K.,** Ilisson, T., Jõgiste, K., Tukia, H., Möls, T. "Coarsne woody debris decay dynamics in two windthrow areas in East – Estonia". In International Workshop on the scale of natural disturbances from tree to stand. 28-30 September 2005. Palanga, Lithuania.

16.05.2006. **Köster, K.,** Ilisson, T., Jõgiste, K. "The regeneration development in storm damaged areas with different damage severity and nutrient (NPK) content in soil". In conference on Natural disturbance-based silviculture: Managing for complexity. 14-18 May 2006. Rouyn-Noranda (Quebec) Canada.

12.09.2006. **Köster, K.,** Ilisson, T., Jõgiste, K. "Nutrient stores and dynamics of coarse woody debris in windthrow areas". In workshop of the SNS (Nordic Forest Research Co-operation Committee) network Natural Disturbance Dynamics Analysis for Forest Ecosystem Management, "Disturbances at the landscape level: ecology and management". 11.-15.09.2006. Tromso, Norway.

08.08.2007. **Köster, K.,** Metslaid, M., Jõgiste K., and Ilisson, T. "Species influence to the mechanism of wind damage in mixed stands". In IUFRO Wind and Trees Conference August 5-9, 2007. Vancouver, Canada.

04.10.2007. **Köster, K.,** Metslaid, M., Jõgiste, K., Voolma, K., Laarmann, D. "Assessment of tree mortality after windthrow using photo-derived data". In workshop of the SNS (Nordic Forest Research Co-operation Committee) network Natural Disturbance Dynamics Analysis for Forest Ecosystem Management, "Disturbance regimes in changing environment". 03.– 06. October 2007. Tukums, Latvia

06.10.2008. **Köster, K.,** Jõgiste, K., Vodde, F., Zettur, I. “The regeneration development in storm damaged areas with different damage severity and nutrient (NPK) content in soil”. In workshop of VII international SNS Natural Disturbance Dynamics Analysis for Forest Ecosystem network “Mixed forest disturbances in boreal and temperate zone”. 06-10. October, Bialowieza, Poland.

25.10.2008. **Köster, K.,** Jõgiste, K., Vodde, F., Zettur, I. “The regeneration development in storm damaged areas with different damage severity and nutrient (NPK) content in soil”. In IUFRO 1.05 (uneven-aged silviculture group) conference “Feasibility of Silviculture of Complex Stand Structures”. 24.-27. October in Shizuoka, Japan

Local conferences and meetings

22.04.2004. “Tormikahjustuste iseloomu mõjutavad tegurid Tudu ja Halliku metskonna kaitsealadel”. EPMÜ Metsandusteaduskonna magistrantide ja doktorantide ettekannetepäeval.

VIIS VIIMAST KAITSMIST

MAREK METSLAID

GROWTH OF ADVANCE REGENERATION
OF NORWAY SPRUCE AFTER CLEARCUT

HARILIKU KUUSE EELUUENDUSE KASV LAGERAIE JÄRGSELT
Juhendajad: Vanemteadur **Kalev Jõgiste**, Professor **Eero Nikinmaa**
August 29, 2008.

IVI JÕUDU

EFFECT OF MILK PROTEIN COMPOSITION AND GENETIC
POLYMORPHISM ON MILK RENNET COAGULATION PROPERTIES

PIIMA VALGULISE KOOSTISE JA GENEETILISE POLÜMORFOSMI
MÕJU PIIMA LAAPUMISOMADUSTELE
Juhendajad: Prof. **Olav Kärt,** Prof. emer. **Olev Saveli,**
Scientific consultant **Merike Henno**, PhD
August 29, 2008.

SIMON BELL

LANDSCAPE CHANGE, LANDSCAPE
PERCEPTION AND THE LATVIAN COUNTRYSIDE.

MAASTIKUMUUTUSTE JA MAASTIKUTAJU
ANALÜÜS LÄTI MAAPIIRKONDADES
Juhendaja: Prof. **Kalev Sepp**
Märts 17, 2009

ELE VOOL

YIELD AND FRUIT QUALITY OF SOME SELECTED
BRAMBLE (RUBUS) SPECIES.
PEREKONNA MURAKAS (RUBUS) MÕNEDE LIIKIDE
SAAGIKUS JA VILJADE KVALITEET
Juhendaja: Prof. **Kadri Karp**
Märts 30, 2009

JAAK SAMARÜTEL

RELATIONSHIPS BETWEEN ENERGY BALANCE ESTIMATES,
LUTEAL ACTIVITY AND FERTILITY IN ESTONIAN HOLSTEIN COWS.

ENERGIA- JA AINEVAHETUSSEISUNDI NÄITAJATE SEOSED
LUTEAALAKTIIVSUSE JA SIGIMISEGA EESTI HOLSTEINI LEHMADEL.
Juhendajad: Prof. **Olav Kärt**, Prof. **Andres Valdmann**, Vanemteadur **Katri Ling**
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