



Does clear-cut harvesting accelerate initial wood decomposition? A five-year study with standard wood material



L. Finér^{a,*}, M. Jurgensen^b, M. Palviainen^c, S. Piirainen^a, D. Page-Dumroese^d

^a Natural Resources Institute Finland, Box 68, FI-80101 Joensuu, Finland

^b Michigan Technological University, School of Forest Resources and Environmental Science, 1400 Townsend Drive, Houghton, MI 49931, USA

^c University of Helsinki, Department of Forest Sciences, Box 27, 00014 Helsinki, Finland

^d USDA Forest Service, Rocky Mountain Research Station, Forestry Science Laboratory, 1221 S. Main Street, Moscow, ID 83843, USA

ARTICLE INFO

Article history:

Received 11 January 2016

Received in revised form 30 March 2016

Accepted 31 March 2016

Available online 9 April 2016

Keywords:

Coarse woody debris

Decay

Nitrogen

Pinus sylvestris

Pinus taeda

Populus tremuloides

Soil preparation

Soil temperature

ABSTRACT

Coarse woody debris (CWD) serves a variety of ecological functions in forests, and the understanding of its decomposition is needed for estimating changes in CWD-dependent forest biodiversity, and for the quantification of forest ecosystem carbon and nutrient pools and fluxes. Boreal forests are often intensively managed, so information is needed on the effects of timber harvesting on wood decomposition, and the factors controlling the decomposition process. Therefore, decomposition of standard wood stakes of Scots pine, loblolly pine, and aspen were monitored in an uncut forest and in an adjacent clear-cut in Finland. Stakes of each species were placed horizontally on the top of the surface organic layer, at the organic layer–mineral soil interface, and vertically in the mineral soil to depth of 20 cm in both the uncut forest and in the clear-cut. Five stakes of each tree species were taken every year from each stake location for five years. Mass loss of wood stakes from all three species was greater in the clear-cut than in the uncut forest during the five-year decomposition period, losing an average 59.8% of their mass in the clear-cut, which was greater than mass loss by both pines ($19.8 \pm 3.0\text{SE}\%$) and aspen ($43.3 \pm 5.1\text{SE}\%$) in the uncut forest. Aspen wood stakes decomposed faster than both Scots and loblolly pine stakes in the uncut forest during the whole study period, but after two years there were no differences between the three species in the clear-cut. In the uncut forest, mass loss of stakes on the surface of the organic layer was 6–10% faster than those at the mineral soil interface or in the mineral soil. In contrast, mass loss of stakes, placed on the top of organic layer in the clear-cut was 32–35% lower than those deeper in the soil probably due to low moisture conditions at the soil surface. Wood stake mass loss was positively correlated with the sum of soil temperature degree days ($r \geq 0.94$). In the uncut forest mass loss was positively correlated with wood stake N accumulation, indicating that N availability was also a factor in decomposition before harvesting. Our study indicates that wood decomposition in this boreal forest is more sensitive to increased soil temperatures and N availability after clear-cut harvesting than found in earlier studies.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

In forest ecosystems coarse woody debris (CWD) forms heterogeneous group of residues consisting of standing dead trees, fallen logs and branches, stumps and coarse roots located either above- or below-ground. CWD serves a variety of ecological functions by providing a habitat for a diverse group of plants, including tree seedlings, animals and microorganisms (Zhou et al., 2007), and so has a key role in maintaining the biodiversity of boreal forests.

* Corresponding author.

E-mail addresses: leena.finer@luke.fi (L. Finér), mjurgjen@mtu.edu (M. Jurgensen), sirpa.piiirainen@luke.fi (S. Piirainen), ddumroese@fs.fed.us (D. Page-Dumroese).

CWD also plays an important role in forest ecosystem carbon (C) and nutrient cycling and soil formation (e.g., Laiho and Prescott, 2004). Thus the understanding of CWD decomposition is needed for estimating more accurate quantification of forest ecosystem C and nutrient pools and fluxes. National greenhouse gas inventories under international conventions also require estimation of changes in dead wood C stocks (e.g., Moroni et al., 2015). Reliable estimate of CWD decomposition, and its response to changes in temperature and moisture, is of prime importance in developing biogeochemical models, and predicting current and future C sinks and sources of forest ecosystems.

In pristine boreal forests of Europe the amount of above-ground CWD varies from 60 to 110 m³ ha^{−1}, and is reduced by 70–98% in managed forests due to shorter rotations, intensive harvesting of

logging residues for biofuel, and the removal of dying trees to avoid pest insect outbreaks (Fridman and Walheim, 2000; Siitonen et al., 2000). Below-ground CWD consists of stumps and roots, but also above-ground tree fractions, which have been gradually buried in soil due to litterfall deposition and overgrowth of mosses. Below-ground CWD is often neglected in inventories and studies, so there are relatively few estimates of its pool size. However, existing studies indicate that below-ground CWD is usually 20–30% of the above-ground CWD in coniferous forests (Moroni et al., 2015). Clear-cutting is a common practice in European boreal forests, increasing the amount of above-ground CWD by 60–80 m³ ha⁻¹ (Hakkila, 1989), but would also greatly increase the below-ground CWD pool size as well.

In uncut cool, humid boreal forests C and nutrients are released from both above- and below-ground CWD at a slow rate, requiring tens to hundreds of years for full decomposition (Palviainen et al., 2008, 2010, 2015; Russell et al., 2014; Shorohova and Kapitsa, 2014). The decomposition rate of CWD is dependent on climatic regimes, especially temperature and moisture (Chen et al., 2000; Yatskov et al., 2003; Janisch et al., 2005; Moroni et al., 2009; Shorohova et al., 2012), as well as wood quality and the type of microbial communities present (e.g., Laiho and Prescott, 2004; Zhou et al., 2007; Kubartová et al., 2015). Surface CWD in uncut boreal forests is easily buried under litter and growing mosses, which increases its moisture content and decreases temperature (Moroni et al., 2015). Anaerobic soil conditions may develop with increasing soil moisture levels, preventing decomposition by both white-rot and brown-rot fungi (Basidiomycetes), and leading to the dominance of less effective soft-rot fungi (Ascomycetes) and bacteria (Moroni et al., 2015). Clear-cutting and post-harvest soil preparation increase soil temperatures (Kubin and Kempainen, 1994), which can accelerate CWD decomposition rates. However, increased evaporative water loss from the soil surface after clear-cutting can reduce wood decomposition (Chen et al., 2000; Laiho and Prescott, 2004; Zhou et al., 2007; Crockatt and Bebb, 2015).

The results of clear-cutting studies on decomposition of leaf and other fine litter components are variable, and have shown an increase (Prescott et al., 2000; Lee et al., 2002; Kim et al., 1996; Prescott, 1997), no effect, or decreased decomposition rates (Kim et al., 1996; Prescott, 1997; Lytle and Cronan, 1998; Palviainen et al., 2004). Preliminary results of a chronosequence study by Janisch et al. (2005) in temperate forests indicate that above-ground CWD decomposition is higher in clear-cuts than in intact forests, in contrast to the results of Crockatt and Bebb (2015), who found that wood decomposition rate increases with distance when moving to the forest from the forest opening. These differences are likely due to differences in microclimatic conditions. How decomposition of CWD changes after clear-cutting, and the roles of temperature and moisture conditions are still poorly documented.

The total and available nutrients in CWD and soil, especially nitrogen (N) are also important factors controlling decomposition (e.g., Weedon et al., 2009; Risch et al., 2013; Shorohova and Kapitsa, 2014). CWD has high lignin content and C:N ratios, which limit the activity of fungi and bacteria in wood decomposition (Merrill and Cowling, 1965; Berg and McClaugherty, 2003). The C released as CO₂ during CWD decomposition is quickly lost into the atmosphere, whereas N either moves into the surrounding soil (Krankina et al., 1999; Palviainen et al., 2008), or is retained in the wood and accumulates over several decades (Laiho and Prescott, 2004; Palviainen et al., 2010). In most boreal forests N is of limited supply (Nohrstedt, 2001), but clear-cutting and subsequent site preparation increases soil N mineralization and availability by adding large amounts of easily decomposable organic matter to the forest floor (Smolander et al., 2000; Palviainen et al., 2004; Smolander and Heiskanen, 2007). Laboratory studies have shown

that increased soil N availability accelerates decomposition of surface and buried wood (van der Wal et al., 2007). However, it is still unclear whether increased N availability after clear-cutting would have similar impacts on above- and below-ground CWD decomposition rates in forests.

The chemical composition of wood can vary widely among different tree species, which can affect their decomposition rate (e.g., Laiho and Prescott, 1999, 2004; Palviainen et al., 2008, 2010; Strukelj et al., 2013). Compared to conifers, the wood of broadleaf trees usually has higher amounts of N, lower lignin concentrations, and lower C:N ratios. Decomposition rates of above-ground conifer wood are often lower than the wood of broadleaf trees in temperate and boreal forests (Palviainen et al., 2008, 2010; Strukelj et al., 2013; Shorohova and Kapitsa, 2014). However, relatively little is known on species-specific response of below-ground wood to clear-cut harvesting and site preparation.

Therefore, we conducted a five year study in an eastern Finland boreal forest to assess the impacts of clear-cut harvesting and site preparation on the wood decomposition of three tree species. The objectives of our study were to answer three questions: (a) how does clear-cutting and subsequent site preparation affect wood decomposition of these species, (b) how does location in the soil affect wood decomposition, and (c) how does soil micro-climate and N levels in both wood and soil affect decomposition.

Mass loss of wood from Scots pine (*Pinus sylvestris* L.) and two non-native tree species, trembling aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda* L.) were used as an index of decomposition. Wood size and chemical properties have variable effects on decomposition rates (van der Wal et al., 2007), which we reduced by using standard wood stakes cut from knot-free, #1 grade boards. Non-native trembling aspen and loblolly pine were used in this study because these two species are standard substrates in a global wood decomposition project (Jurgensen et al., 2006; Risch et al., 2013).

We hypothesized that: (1) wood stake mass loss is greater in the clear-cut than in the uncut forest due to higher soil temperatures and increased soil N availability, (2) wood stake mass loss would be greater in the mineral soil than on the top of the surface organic layer due to less variable temperature and moisture conditions, and (3) aspen stakes will lose more mass than both Scots pine and loblolly pine stakes due to higher wood N contents.

2. Material and methods

2.1. Study site

The study was carried out in the Kangasvaara experimental catchment (56 ha) in eastern Finland (63°51'N, 28°58'E), which has been monitored to determine the effects of clear-cutting and soil preparation on nutrient fluxes and stocks (Finér et al., 1997). The long-term (1981–2010) mean annual air temperature for the area is +2.3 °C and precipitation 527 mm, of which about 200 mm is snowfall (Pirinen et al., 2012). The forest in the catchment is dominated by Norway spruce (*Picea abies* (L.) H. Karst.), but Scots pine, white and silver birch (*Betula pubescens* Ehrh. and *Betula pendula* Roth) and European aspen (*Populus tremula* L.) are also present. The site is classified as a medium rich *Vaccinium-myrtillus*-type (according to the classification by Cajander (1949)), and the soil as a haplic podzol (IUSS Working Group WRB, 2007) developed in sandy till having a clay content of <2% (by mass) and stone content of 28% (by volume). The underlying bedrock (granodiorite) is at a depth of 2 m.

In August 1996, 8.3 ha of the forest in the catchment was clear-cut and the rest remained intact. In September 1998 the clear-cut area was harrowed with a tractor-back mounted disc-plow and

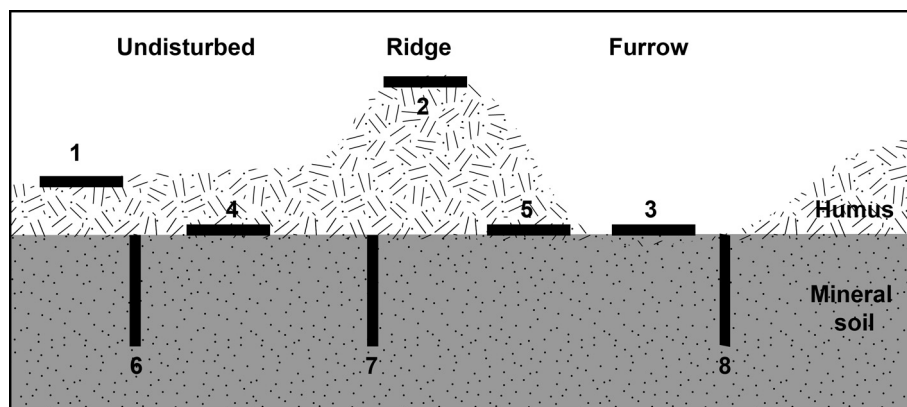


Fig. 1. Location of surface (1–3), surface organic layer–mineral soil interface (3–5), and mineral soil (6–8) wood stakes in micro-sites in the clear-cut. The location of the stakes in the uncut forest was similar to that in the undisturbed micro-site in the clear-cut.

Table 1

Soil C and N concentrations and C:N ratio in the uncut forest and in different micro-sites of the clear-cut at the beginning of the study (Piirainen, unpublished data).

Treatment	Micro-site	Soil horizon	Thickness (cm)	pH	C (%)	N (%)	C:N ratio
Forest	Undisturbed	Organic	4.1	3.71	40.41	1.048	39
		E	10.2	4.05	1.39	0.071	20
		B	12.6	4.70	2.35	0.115	20
Clear-cut	Undisturbed	Organic	3.8	4.00	32.00	0.890	36
		E	8.1	4.26	1.27	0.063	20
		B	11.8	4.92	1.79	0.082	22
	Ridge	Organic	9.0	4.36	14.82	0.434	34
		E	8.1	4.40	1.33	0.063	21
		B	11.9	4.95	1.62	0.080	20
	Furrow	E	6.0	4.42	1.57	0.073	21
		B	14.7	5.02	1.57	0.075	20

planted with one-year-old potted Scots pine seedlings in the following June. The harrowing resulted in the formation of three kinds of micro-sites: (1) undisturbed strips (45% of the area), (2) shallow furrows (~7 cm in depth) with exposed mineral soil surface (30% of the area), and (3) low ridges, app. 9 cm higher than the undisturbed soil, and formed by the overturning the surface organic layer and understory vegetation from the furrows on top of adjacent undisturbed soil (25% of the area) (Fig. 1). Soil chemical properties of the uncut forest and on the three micro-sites in the clear-cut are presented in Table 1. The thickness of the surface organic layer in the uncut forest was 4.1 cm. Surface organic layer thickness on the undisturbed micro-sites in the clear-cut had decreased to 3.8 cm at the beginning of our study, and did not change during the next five years. Surface organic layer thickness on the ridges was highly variable across the clear-cut, averaging 9.0 cm, which decreased to 6.3 cm during the study period. The furrow micro-sites had little (<1 cm) to no surface organic layer.

2.2. Wood material

Wood stakes placed on and in surface organic layers (size $2.5 \times 2.5 \times 15$ cm) and in mineral soil ($2.5 \times 2.5 \times 20$ cm) were cut from kiln-dried, knot free aspen, Scots pine, and loblolly pine “mother” stakes ($2.5 \times 2.5 \times 50$ cm). The pine stakes were made of sapwood. Two field “daughter” stakes were cut from each mother stake, and the remaining center sections (10 or 15 cm) were used to measure initial wood chemical and physical properties (t_0) of the daughter field stakes (see Jurgensen et al., 2006). The top of each mineral soil stake was treated with a wood sealer to reduce moisture loss after installation.

2.3. Experimental design

In June 2001 three plots ($8 \text{ m} \times 54 \text{ m}$) were established in the uncut forest and on the three micro-sites in the clear-cut. Three 50 m lines, 2 m apart were laid out on each plot. In the uncut forest plots, 75 stakes (25 surface, 25 interface, 25 mineral) of each tree species were installed, as shown in Fig. 1 ($n = 675$ stakes, 3 plots \times 3 locations \times 3 wood species \times 25 stakes). In the clear-cut 25 surface, 25 interface, and 25 mineral stakes of each tree species were installed on each micro-site plot (Fig. 1, $n = 1800$ stakes, 3 plots \times 8 locations \times 3 wood species \times 25 stakes). To reduce soil compaction and damage to the mineral soil stakes, during installation, the surface organic layer was removed, the stakes were placed level with the mineral soil surface in holes made by a square coring tool, and the organic layer replaced. Five stakes of each tree species from each location were taken from all uncut and clear-cut plots in June or July ($n = 495$ stakes) for five years (2002–2006). All stakes were air-dried, and sent to the School of Forest Resources and Environmental Science at the Michigan Technological University, Houghton, MI for processing.

In the laboratory, all stakes were dried at 105°C for 48 h and weighed. Wood decomposition was measured by comparing dry weights (mass) of collected field stakes to the weights of mother stake control sections. Changes in C and N in mineral soil stakes during the decomposition process were determined by measuring the C and N contents in a subsample of aspen and loblolly pine stakes taken from the 5 cm soil depth in different years, as compared to C and N contents in the mother stake control sections. Field and control blocks were passed through a Wiley Mill (0.40 mm screen), ground in a ball mill, and C and N concentrations measured on a LECO CHN-1000 (Leco Corp., St. Joseph, MI).

machine at the USDA Forest Service, Rocky Mountain Research Station, Moscow, ID.

2.4. Climate and microclimate data

Sensors to measure volumetric soil moisture content (Theta Probe ML2x and ML1x; Delta-T Devices) and soil temperature (Campbell 105T Thermocouple) were placed in the surface organic layer and at two mineral soil depths in one uncut forest plot, and in one plot of each clear-cut micro-site, except for furrows, which had no surface organic layer. Sensor depths were 1.5 cm in the surface organic layers of uncut forest and clear-cut undisturbed micro-site, 4.5 cm in the ridge, and in mineral soil at 15 and 25 cm depths.

Table 2

The relationship of wood stake mass loss to the clear-cut treatment and other fixed factors and their interactions in a mixed model.

Factor	Degrees of freedom	F-value	Significance, p-value
Intercept	1	9749.0	<0.001
Treatment	1	475.0	<0.001
Time	4	309.2	<0.001
Species	2	93.8	<0.001
Location	2	33.6	<0.001
Treatment * Location	2	133.1	<0.001
Treatment * Species	2	15.0	<0.001
Treatment * Time	4	9.3	<0.001
Species * Location	4	1.1	0.336
Species * Time	8	0.7	0.734
Time * Location	8	0.9	0.558
Treatment * Time * Location	8	4.2	<0.001
Treatment * Species * Location	4	1.1	0.354
Species * Time * Location	16	1.0	0.549
Species * Treatment * Time	8	3.6	<0.001
Species * Treatment * Time * Location	20	0.7	0.791

2.5. Calculations and statistical tests

The decomposition rate constant k (year^{-1}), was calculated for the different decomposition periods with the negative exponential decomposition function (1), to be able to compare the results with the other studies, although this function might not be the best to describe the decomposition dynamics (Fraver et al., 2013):

$$k = \ln(DW_0/DW_t)/t, \quad (1)$$

where DW_0 is the initial dry mass prior to the insertion and DW_t is the dry mass at the end of the period t , and t is the length of the decomposition period in years.

A mixed linear model was first used to test the differences in mass loss (%) between the different micro-sites created by soil preparation after clear-cutting. Tree species (Scots pine, loblolly pine, aspen), micro-site (undisturbed, ridge, furrow), stake location (surface, interface, mineral soil; Fig. 1) and incubation time (1, 2, 3, 4, 5 years), and their interactions were defined as fixed factors, while plot (3) was defined as a random factor. Thereafter mixed linear models were used for testing the differences in mass loss and decomposition rate constant k (year^{-1}) between the uncut forest and clear-cut, tree species, stake locations, and sampling years. Treatment (clear-cut vs. forest), tree species, stake location, and incubation time, and their interactions were defined as fixed factors, while plot was defined as a random factor. As the interaction between treatment and location was found to be significant (p -value < 0.05), the tests were separated by the treatments. Mass loss was square root -transformed before the analyses to normalize the data. Post-test comparisons were made using Bonferroni's test, and correlation (Pearson) analyses were used to study the relationships among mass loss, temperature conditions, and N gains of the stakes. The differences in the initial C and N concentrations of the wood stakes of the three tree species were tested by one-way

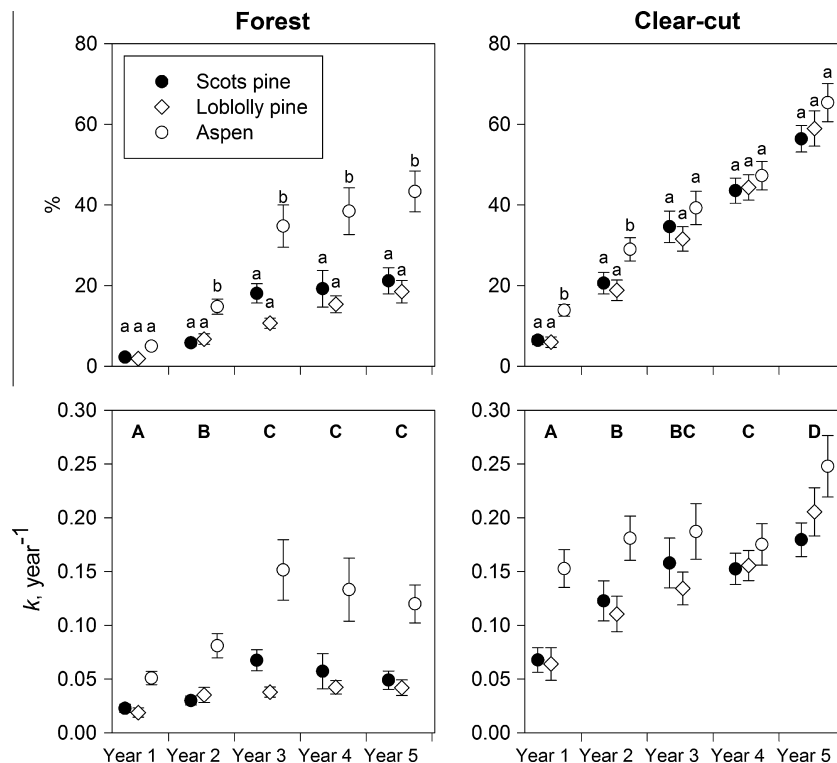


Fig. 2. Mean mass losses, % and decomposition rate constants, k , (\pm standard errors) of all Scots pine, loblolly pine and aspen wood stakes in the forest ($n = 9$) and in the clear-cut ($n = 24$) during the five-year study period. Different lower case letters indicate statistically significant differences ($p < 0.05$) among the species in each year. The upper case letters indicate significant differences ($p < 0.05$) among years with all three tree species combined.

Table 3

The relationship of wood stake mass loss on the clear-cut to micro-site and other fixed factors and their interactions in a mixed model.

Factor	Degrees of freedom	F-value	Significance, p-value
Intercept	1	17415.6	<0.001
Micro-site	2	0.5	0.598
Time	4	415.0	<0.001
Species	2	30.5	<0.001
Location	2	296.4	<0.001
Micro-site * Species	4	0.51	0.723
Micro-site * Location	3	18.6	<0.004
Micro-site * Time	8	0.7	0.685
Species * Location	4	1.5	0.195
Species * Time	8	2.6	0.007
Time * Location	8	5.2	<0.001
Micro-site * Time * Location	12	0.6	0.881
Species * Time * Location	20	1.0	0.493
Species * Micro-site * Time	16	0.7	0.806
Species * Micro-site * Time * Location	30	0.8	0.774

analysis of variance. All statistical analyses were performed with the PASW Statistics 22.0 statistical package (IBM SPSS, Chicago, Illinois, USA).

3. Results

3.1. Effects of clear-cutting and site preparation on mass loss

The mass loss of wood stakes was greater in the clear-cut than in the uncut forest for all species in all years (Table 2, Fig. 2), except the mass loss of aspen stakes removed in 2004 after three years of incubation ($p = 0.11$). In the uncut forest the mass loss increased during the first three years of the study, and then showed very little change during the last two years, whereas in the clear-cut the stakes continued to lose mass during the entire five year period. Over the five years of the study, the three stake species combined lost 59.8% of their mass in the clear-cut with little difference among species at the end of the period (Fig. 2). Mass loss for stakes of the two pine species was three times greater and 1.4 times greater for aspen in the clear-cut than in the uncut forest.

Site preparation treatment in the clear-cut did not affect mass loss, since the micro-sites did not have any significant interaction between species or incubation time (Table 3). However, a significant interaction was present between micro-site and stake location, indicating that wood stakes placed on the top of furrows (without organic layer) decomposed faster than those on the top of the surface organic layer on ridge and undisturbed micro-sites (Table 4).

Aspen stakes decomposed faster than both pine species in the uncut forest and clear-cut during the first two years, but thereafter the differences among the three species levelled off in the clear-cut (Fig. 2). The mass losses and decomposition rate constants, k of the two pine species in the forest or in the clear-cut did not differ during any study period. Mean annual decomposition rate constants (year^{-1}) for the whole five year study period were $0.049 \pm 0.0085\text{SE}$ for all Scots pine stakes, $0.042 \pm 0.0073\text{SE}$ for all loblolly pine stakes, and $0.119 \pm 0.018\text{SE}$ for all aspen stakes in the uncut forest. In contrast, k values were 3.7 ($0.180 \pm 0.015\text{SE}$), 4.9 ($0.206 \pm 0.022\text{SE}$) and 2.1 ($0.248 \pm 0.029\text{SE}$) times higher in the clear-cut, respectively.

3.2. Differences in mass loss among stake locations

The mass loss differed significantly among stake locations in both the uncut forest ($F = 10.76$, $p < 0.001$), and in the clear-cut ($F = 289.5$, $p < 0.001$; Fig. 3), and no significant interactions were found between stake location and wood species (Table 2). During

Table 4

Mass loss of wood stakes in the clear-cut at the end of the five-year study period (mean \pm standard error). Lower case letters indicate significant differences across wood stake locations within each micro-site. Upper case letters indicate significant differences across micro-sites within each location. Number of observations is 8, except 9 for mineral soil.

Micro-site	Location	Mass loss (%)
Undisturbed	Surface	$39.6 \pm 3.0^{\text{aA}}$
	Interface	$71.7 \pm 2.8^{\text{bA}}$
	Mineral soil	$74.8 \pm 3.1^{\text{bA}}$
Ridge	Surface	$30.7 \pm 3.4^{\text{aA}}$
	Interface	$76.0 \pm 4.1^{\text{bA}}$
	Mineral soil	$72.4 \pm 3.5^{\text{bA}}$
Furrow	Surface	$45.6 \pm 5.7^{\text{aB}}$
	Mineral soil	$64.0 \pm 2.8^{\text{bA}}$

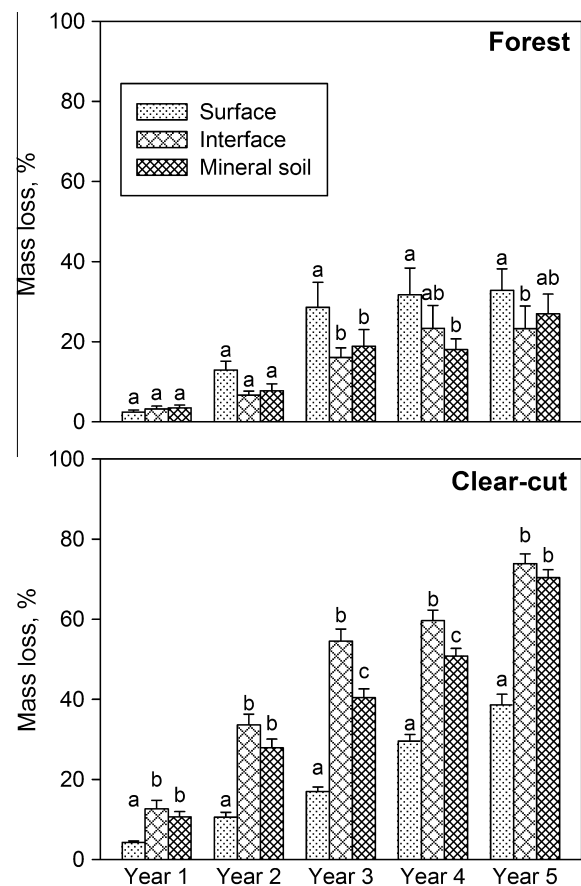


Fig. 3. Mean mass loss (\pm standard error) of the wood stakes at different locations in the uncut forest and in the clear-cut during the five years. Different letters indicate statistically significant differences ($p < 0.05$) between the locations.

the five-year period the mass loss of stakes placed on the top of organic layer in the uncut forest was 6–10% greater than those located at the mineral soil interface or in the mineral soil. In contrast, mass loss of wood stakes placed on the top of organic layers in the clear-cut micro-sites was 32–35% lower than those at the mineral soil interface or in the mineral soil. There were no differences in the mass loss between stakes located at the mineral soil interface and in the mineral soil in either the uncut forest or the clear-cut at the end of the five-year period.

3.3. Changes in wood C and N contents

As shown in Table 5, the initial C concentrations of Scots pine and loblolly pine stakes were significantly higher than those of

Table 5

Initial C and N concentrations and C:N -ratio (mean \pm standard error) of aspen, loblolly pine and Scots pine stakes (n = number of stakes) and the results of ANOVA showing the differences among species. The different letters indicate differences among species according to the Bonferroni's test ($p < 0.05$).

Species	C (%)	N (%)	C:N ratio	n
Aspen	46.4 \pm 0.08 ^a	0.121 \pm 0.003 ^a	391 \pm 10.4 ^a	33
Loblolly pine	47.6 \pm 0.08 ^b	0.104 \pm 0.003 ^b	473 \pm 14.2 ^b	33
Scots pine	47.8 \pm 0.08 ^b	0.112 \pm 0.003 ^c	432 \pm 9.5 ^c	32
	$F = 7.5$ $p < 0.001$	$F = 9.9$ $p < 0.001$	$F = 12.7$ $p < 0.001$	

Table 6

Changes in C and N contents (mean \pm standard error) for aspen, loblolly pine and Scots pine wood stakes at the 5 cm mineral soil depth at the end of one, three, and five years incubation. ($n = 3$, except 1 for loblolly pine and 2 for Scots pine in 2006 in uncut forest).

Species	C loss (%)		N gain (%)	
	Forest	Clear-cut	Forest	Clear-cut
2002				
Aspen	-4.6 \pm 1.2	-12.8 \pm 1.9	11.5 \pm 16.7	43.5 \pm 11.4
Loblolly pine	-2.2 \pm 0.8	-5.3 \pm 2.4	-4.1 \pm 0.9.1	27.0 \pm 17.8
Scots pine	-3.0 \pm 0.5	-7.4 \pm 2.3	32.5 \pm 13.6	56.9 \pm 14.0
2004				
Aspen	-31.5 \pm 12.2	-41.1 \pm 0.8	89.1 \pm 42.9	34.9 \pm 15.7
Loblolly pine	-9.0 \pm 4.5	-37.2 \pm 7.1	29.9 \pm 19.6	30.5 \pm 23.8
Scots pine	-20.2 \pm 5.6	-43.2 \pm 5.4	54.5 \pm 29.5	54.7 \pm 18.4
2006				
Aspen	-51.3 \pm 5.0	-69.2 \pm 1.0	39.6 \pm 10.4	42.6 \pm 10.5
Loblolly pine	-12.0	-58.8 \pm 10.4	8.6	10.2 \pm 7.2
Scots pine	-44.7 \pm 2.3	-69.0 \pm 3.5	18.9 \pm 44.8	12.5 \pm 10.4

aspen, and all species showed a change over the five-year period (Table 6). Initially, aspen wood had significantly higher N concentrations than the wood of pines, but in contrast to C, N contents of all three species increased during the decomposition process. As expected, C loss in all three species closely paralleled mass loss ($r = 0.99$, $p < 0.001$). Nitrogen accumulation in the stakes during decomposition was variable across the uncut forest and the clear-cut. Nitrogen accumulation in the stakes of all three species had a positive correlation with the C loss in the uncut forest ($r = 0.55$, $p = 0.01$). In contrast, there was no significant correlation between the N accumulation and the C loss in any stake species in the clear-cut ($r = 0.02$, $p = 0.89$).

3.4. Soil micro-climate

Soil temperature and moisture conditions differed between the uncut forest and the clear-cut. Soil moisture content was higher and soil temperature and accumulated degree days (threshold value 5 °C) lower in the uncut forest than in the clear-cut (Tables 7 and 8). Overall, mass loss differed among the pines and aspen, but all increased in relation to the accumulation of soil temperature ($r \geq 0.94$, $p < 0.001$) (Fig. 4).

4. Discussion

4.1. Mass loss and decomposition rate

As hypothesized, mass loss of wood stakes was greater in the clear-cut than in the uncut forest, and was almost solely due to the lower soil temperatures in the uncut forest. The sum of accumulated degree days in soil (temperature sum, above 5 °C) correlated positively with the mass loss from the stakes both in the uncut forest and clear-cut. The temperature sensitivity of wood

Table 7

Mean (\pm standard error) annual moisture (% of volume,) content, temperature and temperature sum (degree days, threshold temperature 5 °C) in the middle of the organic layer and at 15 and 25 cm mineral soil depths in the uncut forest and in different micro-sites on the clear-cut averaged over five frost-free seasons. Different lower case letters indicate statistically significant differences among layers within each micro-site, and the upper case letters among micro-sites within each soil layer in the clear-cut.

Micro-site	Soil layer	Soil moisture (%)	Soil temperature (°C)	Soil temperature sum, (degree days) (°C)
Forest				
Undisturbed	Organic	0.23 \pm 0.015 ^a	9.6 \pm 0.25 ^a	699 \pm 29 ^a
	15 cm	0.29 \pm 0.009 ^b	9.2 \pm 0.23 ^b	627 \pm 26 ^b
	25 cm	0.31 \pm 0.010 ^b	8.5 \pm 0.22 ^c	529 \pm 31 ^c
Clear-cut				
Undisturbed	Organic	0.18 \pm 0.012 ^{aA}	11.9 \pm 0.30 ^{aA}	1040 \pm 34 ^{aA}
	15 cm	0.28 \pm 0.007 ^{bA}	11.6 \pm 0.29 ^{bA}	990 \pm 33 ^{bA}
	25 cm	0.19 \pm 0.004 ^{cA}	10.7 \pm 0.25 ^{cA}	840 \pm 28 ^{cA}
Ridge	Organic	0.16 \pm 0.019 ^{aA}	12.8 \pm 0.22 ^{aA}	1179 \pm 18 ^{aB}
	15 cm	0.18 \pm 0.020 ^{aB}	11.5 \pm 0.20 ^{bA}	979 \pm 15 ^{bA}
	25 cm	0.13 \pm 0.012 ^{aB}	10.7 \pm 0.16 ^{cA}	854 \pm 13 ^{cA}
Furrow	25 cm	0.21 \pm 0.011 ^A	11.0 \pm 0.15 ^A	911 \pm 14 ^A

Table 8

The relationship of annual soil moisture, soil temperature, and temperature sum to clear-cut treatment, soil layer, and their interaction in ANOVA.

Factor	Degrees of freedom	F-value	Significance, p-value
Soil moisture			
Intercept	1	1578.0	<0.001
Treatment	1	50.8	<0.001
Soil layer	2	9.7	<0.001
Treatment * Soil layer	2	7.8	<0.001
Soil temperature			
Intercept	1	4068.9	<0.001
Treatment	1	54.9	<0.001
Soil layer	2	5.8	<0.001
Treatment * Soil layer	2	0.1	0.67
Soil temperature sum			
Intercept	1	5430.0	<0.001
Treatment	1	278.4	<0.001
Soil layer	2	29.0	<0.001
Treatment * Soil layer	2	0.6	0.54

stake decomposition agrees with results from previous short and long-term CWD decomposition studies (e.g., Yin, 1999; Jurgensen et al., 2006; Hermann and Bauhus, 2013; Risch et al., 2013; Russell et al., 2014), although not with all (Yatskov et al., 2003; Mäkinen et al., 2006). However, most of these earlier studies were conducted on above-ground CWD, which may be more sensitive to temperature-related surface soil water loss than wood in the mineral soil. There was a positive correlation between mass loss, C loss and N gain in the uncut forest, which suggests that N availability was also a factor in wood decomposition before harvesting. Arthur and Fahey (1990) and van der Wal et al. (2007) have suggested that both wood decomposition and N accumulation are related to N availability. In contrast there was no significant relationship between the mass loss and N accumulation in the clear-cut. This lack of N impact on wood decomposition in the clear-cut is likely related to increased soil N availability after clear-cut harvesting (Smolander et al., 2000; Piirainen et al., 2002; Palviainen et al., 2004; Smolander and Heiskanen, 2007).

The higher k constants in the clear-cut than in the uncut forest also reflect the large temperature effect on wood decomposition, since the activity of wood-decomposing fungi has been found to increase 1.4–4.8-fold for every 10 °C rise in mean annual

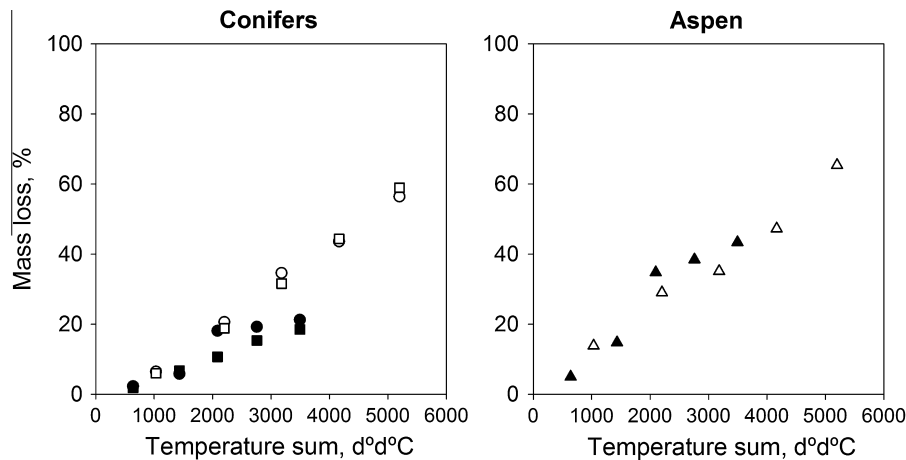


Fig. 4. Relationships between the sum of the soil accumulated degree days and mass loss of Scots pine, loblolly pine, and aspen stakes in the uncut forest and in the clear-cut. (Temperature sum is the accumulated degree days in the undisturbed surface organic layer (threshold value 5 °C)). Mass losses are the means of all locations. Black symbols are for the forest and open symbols for the clear-cut. Scots pine is shown by circle and loblolly pine with square.

temperature (Q_{10} factor) in North American, North Asian, and European forests (Mackensen et al., 2003; Yatskov et al., 2003; Zell et al., 2009; Hermann and Bauhus, 2013). Decomposition rate constants in the uncut forest and in the clear-cut fell within the range found for the early stages of wood decomposition in previous studies (Fig. 5). The difference in mean daily soil temperature between the clear-cut and the uncut forest in our study was only ~ 2.3 °C during the frost-free season (Table 7), which indicates that initial wood decomposition was more temperature sensitive in our study than in earlier studies. That could be because many of our stakes were in mineral soil, had small diameter and did not contain bark, in contrast to CWD in earlier studies (Yatskov et al., 2003; Zell et al., 2009).

Wood mass loss during decomposition is suggested to follow a three phase pattern, the first 5–10 years it is slow, followed by a ten-year-period of rapid decomposition before another long slow period (e.g., Yatskov et al., 2003; Laiho and Prescott, 2004; Palviainen and Finér, 2015). Complete decomposition of CWD usually requires tens or even hundreds of years in forest ecosystems (Mäkinen et al., 2006; Russell et al., 2014; Shorohova and Kapitsa, 2014). Our results are similar to those of Risch et al. (2013), and do not support the presence of an initial slow decomposition phase, since decomposition increased linearly in the clear-cut, and reached high levels within the first five years (Fig. 2). In the uncut forest decomposition increased first, and thereafter

slowed. This could be comparable to the first slow decomposition phase described in the earlier studies, which was attributed to delayed penetration of wood-decomposing organisms into CWD (Laiho and Prescott, 2004). Similar to Risch et al. (2013), we used standardized dried fresh wood stakes, which do not correspond to natural CWD found in the forest. Our stakes were on and under the surface organic layer and in the mineral soil, were of small diameter, and had no bark, factors which enhance fast microbial colonization of wood (Laiho and Prescott, 1999, 2004; Zell et al., 2009). Thus, the differences in the decomposition patterns between the uncut forest and the clear-cut in this study were most probably related to N availability, as discussed earlier.

4.2. Importance of stake location on mass loss

Wood stakes placed on the top of the surface organic layer in the uncut forest decomposed faster than those located deeper in soil, which was most likely due to soil temperature and moisture differences (Fig. 4, Tables 4 and 7). These results agree with those of Risch et al. (2013) from an uncut forest in the Swiss Alps. In addition, the surface stakes in the uncut forest were first covered with growing moss, and eventually buried by tree litterfall, which would lower soil temperature values and increase moisture conditions, both in the surface organic layer and in the underlying mineral soil. In contrast, surface stakes in the clear-cut decomposed slower than those deeper in soil. This wood decomposition pattern was likely controlled by low soil moisture availability at the surface of the organic layer, resulting from higher soil temperatures in the exposed clear-cut. The importance of wood contact with wetter mineral soil is shown by the greater mass loss by stakes placed at the surface organic layer mineral soil interface, and for stakes placed on exposed mineral soil surface in the furrow micro-site. The influence of moisture on CWD decomposition is dependent on prevailing temperature and moisture conditions (Hermann and Bauhus, 2013; Moroni et al., 2015), and moisture content of CWD in clear-cuts have decreased also in the earlier studies to levels too low to sustain decomposition (Yin, 1999; Crockatt and Bebbler, 2015). The soil moisture levels were higher in the uncut forest than in the clear-cut, but the effect of higher water content on wood decomposition could not be separated from the lower soil temperatures in the uncut forest. Post-harvest site preparation treatments had a minor overall effect on wood decomposition, probably because the influences of the differences in temperature and moisture conditions among the micro-sites (Table 7) compensated each other.

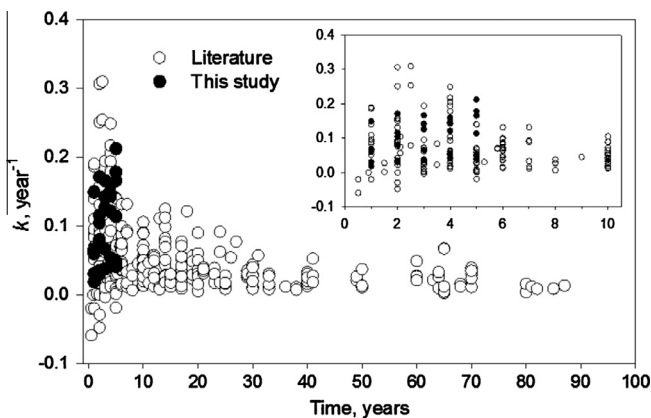


Fig. 5. Decomposition rate constants, k determined for different time periods (for 1–100 years and only for the first 10 years in the smaller figure) for different wood materials of temperate, alpine and boreal forest tree species in studies found in literature (Yin, 1999; Yatskov et al., 2003; Laiho and Prescott, 2004; Mäkinen et al., 2006; Risch et al., 2013) and those measured in this study.

4.3. Differences between tree species

As we hypothesized, the decomposition of the aspen wood stakes proceeded faster than both pines throughout whole five-year-period, which agrees with many previous studies reporting higher decomposition rates of broadleaf species compared to conifers in temperate, alpine and boreal forests (Yatskov et al., 2003; Mäkinen et al., 2006; Shorohova et al., 2008; Shorohova and Kapitsa, 2014; Weedon et al., 2009; Palviainen et al., 2010; Risch et al., 2013; Strukelj et al., 2013). The pines had lower N concentrations and higher C:N ratios than the aspen, factors which have correlated with differences in wood decomposition rates (Laiho and Prescott, 1999; Weedon et al., 2009; Palviainen et al., 2010; Strukelj et al., 2013). Differences in wood decomposition among the three species in the clear-cut were similar to the uncut forest during the first two years, but then leveled off for the rest of the study. The narrowing of mass loss differences between aspen and the pines in the clear-cut over time could be related to higher soil N availability after timber harvesting. Earlier chronosequence studies by Palviainen et al. (2008, 2010) showed that differences in N content between conifers and broadleaf species lasted much longer than in our study, but the wood in these studies was much larger than our wood stakes, and were covered with bark. Species-specific differences have been reported for wood and bark decomposition (Shorohova et al., 2012).

5. Conclusions

The results of our five year study showed that wood stakes of aspen decomposed faster than stakes of both Scots and loblolly pine stakes in the uncut forest during the whole study period, but after two years there were no differences between the three species in the clear-cut. Clear-cut harvesting increased soil temperatures, and resulted in wood stakes of all three species decomposing faster in the clear-cut than in the uncut forest. Mass loss of wood stakes on the surface in the clear-cut was lower than stakes placed at the surface organic layer–mineral soil interface and in the mineral soil, while stakes on top of the surface organic layer in the uncut forest decomposed faster than stakes deeper in the soil. These results indicate wood decomposition on the surface of the clear-cut was limited by the dry conditions and favored by higher moisture conditions in the mineral soil, while lower soil temperatures with increasing soil depth reduced decomposition in the uncut forest. Wood stake mass loss correlated positively with the sum of soil temperature degree days both in the uncut forest and clear-cut. However, stake mass loss correlated positively with wood N accumulation only in the uncut forest, indicating that N availability was a factor in decomposition before harvesting.

Analyses of the wood stakes in our study suggests that CWD located on the soil surface of clear-cuts could provide long term C storage, and CWD incorporated into surface organic layers, especially from conifers, could provide similar benefits in uncut boreal forests. However, below-ground CWD from cut trees (stumps and coarse roots) in clear-cuts would likely decompose more rapidly due to more favorable temperature and moisture conditions in the mineral soil. Our results also indicate that wood decomposition in this boreal forest soil is highly sensitive to increased soil temperatures and N availability after clear-cut harvesting.

Acknowledgements

We thank Prof. Hannu Mannerkoski, PhD Mike Starr and Ms Anita Volkel for the discussions and working with us in the field. We also wish to thank the staff of the laboratories at the Finnish Forest Research Institute, Joensuu, the School of Forest Resources and Environmental Science at the Michigan Technological

University, Houghton, MI and USDA Forest Service, Rocky Mountain Research Station, Moscow, ID for processing the wood stakes and Ms Leena Karvinen for preparing the Figures.

References

- Arthur, M.A., Fahey, T.J., 1990. Mass and nutrient content of decaying boles of an Engelmann spruces – subalpine fir forest, Rocky Mountain National Park, Colorado. *Can. J. For. Res.* 20, 730–737.
- Berg, B., McClaugherty, C., 2003. Plant litter. In: *Decomposition, Humus Formation, Carbon Sequestration*. Springer Verlag, Berlin, p. 286.
- Cajander, A.K., 1949. Forest types and their significance. *Acta For. Fenn.* 56, 72.
- Chen, H., Harmon, M.E., Griffiths, R.P., Hicks, W., 2000. Effects of temperature on carbon respired from decomposing woody roots. *For. Ecol. Manage.* 138, 51–64.
- Crockatt, M.E., Bebbler, D.P., 2015. Edge effects on moisture reduce wood decomposition rate in a temperate forest. *Glob. Change Biol.* 21, 698–707.
- Finér, L., Ahtiainen, M., Mannerkoski, H., Möttönen, V., Piirainen, S., Seuna, P., et al., 1997. Effects of harvesting and scarification on water and nutrient fluxes. A description of catchments and methods, and results from the pretreatment calibration period. Finnish Forest Research Institute, Research Paper 648 (38 p).
- Fraver, S., Milo, A.M., Bradford, J.B., D'Amato, A.W., Kenefic, L., Palik, B.J., et al., 2013. Woody debris volume depletion through decay: implications for biomass and carbon accounting. *Ecosystems* 16, 1261–1272.
- Fridman, J., Walheim, M., 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *For. Ecol. Manage.* 131, 23–36.
- Hakkila, P., 1989. *Utilization of Residual Forest Biomass*. Springer-Verlag, Berlin, Heidelberg, Germany, 568 p.
- Hermann, S., Bauhus, J., 2013. Effects of moisture, temperature and decomposition stage on respiratory carbon loss from coarse woody debris (CWD) of important European tree species. *Scand. J. For. Res.* 28 (4), 346–357.
- IBM SPSS Statistics Version 22, Chicago, Illinois, USA.
- IUSS Working Group WRB, 2007. World Reference Base for Soil Resources 2006, First Update 2007. World Soil Resources Reports No. 103. FAO, Rome.
- Janisch, J.E., Harmon, M.E., Chen, H., Fasth, B., Sexton, J., 2005. Decomposition of coarse woody debris originating from clearcutting of an old-growth conifer forest. *Ecoscience* 12, 151–160.
- Jurgensen, M., Reed, D., Page-Dumroese, D., Laks, P., Collins, A., Mroz, G., Degórski, M., 2006. Wood strength loss as a measure of decomposition in northern forest mineral soil. *Eur. J. Soil Biol.* 43, 23–31.
- Kim, C., Sharik, T.L., Jurgensen, M.F., 1996. Canopy cover effects on mass loss, and nitrogen and phosphorus dynamics from decomposing litter in oak and pine stands in northern Lower Michigan. *For. Ecol. Manage.* 80, 13–20.
- Kubin, E., Kempainen, L., 1994. Effect of soil preparation of boreal spruce forest on air and soil temperature conditions in forest regeneration areas. *Acta For. Fenn.* 244, 56 p.
- Krankina, R.J., Harmon, M.E., Giazkin, 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.
- Kubartová, A., Ottosson, E., Stenlid, J., 2015. Linking fungal communities to wood density loss after 12 years of log decay. *FEMS Microbiol. Ecol.* 91, 1–11. <http://dx.doi.org/10.1092/femsec/fiv032>.
- Laiho, R., Prescott, C.E., 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Can. J. For. Res.* 29, 1592–1603.
- 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.
- Lee, J., Morrison, I.K., Leblanc, J.-D., Dumas, M.T., Cameron, D.A., 2002. Carbon sequestration in trees and regrowth vegetation as affected by clearcut and partial cut harvesting in a second-growth boreal mixed wood. *For. Ecol. Manage.* 169, 83–101.
- Lytle, D.E., Cronan, C.S., 1998. Comparative soil CO₂ evolution, litter decay, and root dynamics in clearcut and uncut spruce-fir forest. *For. Ecol. Manage.* 103, 121–128.
- Mäkinen, H., Hynynen, J., Siitonen, J., Sievänen, R., 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. *Ecol. Appl.* 16 (5), 1865–1879.
- Merrill, W., Cowling, E.B., 1965. Effect of variation in nitrogen content of wood on rate of decay. *Phytopathology* 55, 1067–1068.
- Mackensen, J., Bauhus, J., Webber, E., 2003. Decomposition rates of coarse woody debris: a review with particular emphasis on Australian tree species. *Aust. J. Bot.* 51, 27–37.
- Moroni, M.T., Carter, P.Q., Ryan, A.J., 2009. Harvesting and slash piling affect soil respiration, soil temperature, and soil moisture regimes in Newfoundland boreal forests. *Can. J. Soil Sci.* 89, 343–355.
- Moroni, M.T., Morris, D.M., Shaw, C., Stokland, J.N., Harmon, M.E., Fenton, N.J., Merganičová, K., Merganič, J., Okabe, K., Hagemann, U., 2015. Buried wood: a common yet poorly documented form of deadwood. *Ecosystems* 18, 605–628.
- Nohrstedt, H.O., 2001. Responses of coniferous forest ecosystems on mineral soils to nutrient additions: a review of Swedish experiences. *Scand. J. For. Res.* 16, 555–573.
- Palviainen, M., Finér, L., Kurka, A.-M., Mannerkoski, H., Piirainen, S., Starr, M., 2004. Decomposition and nutrient release from logging residues after clear-cutting of a mixed boreal forest. *Plant Soil* 263, 53–67.

- Palviainen, M., Laiho, R., Mäkinen, H., Finér, L., 2008. Do decomposing Scots pine, Norway spruce and silver birch stems retain nitrogen? *Can. J. For. Res.* 38, 3047–3055.
- Palviainen, M., Finér, L., Laiho, R., Shorohova, E., Kapitsa, E., Vanha-Majamaa, I., 2010. Carbon and nitrogen release from decomposing Scots pine, Norway spruce and silver birch stumps. *For. Ecol. Manage.* 259, 390–398.
- Palviainen, M., Finér, L., 2015. Decomposition and nutrient release from Norway spruce coarse roots and stumps – a 40-year chronosequence study. *For. Ecol. Manage.* 358, 1–11.
- Piirainen, S., Finér, L., Mannerkoski, H., Starr, M., 2002. Effects of forest clear-cutting on the carbon and nitrogen fluxes through podzolic soil horizons. *Plant Soil* 239, 301–311.
- Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J.-P., Karlsson, P., Ruuhela, R., 2012. *Climatological Statistics of Finland 1981–2010*. Finnish Meteorological Institute, Reports, Helsinki.
- Prescott, C.E., 1997. Effects of clear-cutting and alternative silvicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. *For. Ecol. Manage.* 95, 253–260.
- Prescott, C.E., Blevins, L.L., Staley, C.L., 2000. Effects of clearcutting on decomposition rates of litter and forest floor in forests of British Columbia. *Can. J. For. Res.* 30, 1751–1757.
- Risch, A.C., Jurgensen, M.F., Page-Dumroese, D.S., Schütz, M., 2013. Initial turnover rates of two standard wood substrate following land-use change in subalpine ecosystems in the Swiss Alps. *Can. J. For. Res.* 43, 901–910.
- Russell, M.B., Woodall, C.W., Fraver, S., D'Amato, A.W., Domke, G.M., Skog, K.E., 2014. Residence times and decay rates of downed woody debris biomass/carbon in Eastern US forests. *Ecosystems* 17, 765–777.
- Shorohova, E., Kapitsa, E., Vanha-Majamaa, I., 2008. Decomposition of stumps in a chronosequence after clear-felling v. clear-felling with prescribed burning in a southern boreal forest in Finland. *For. Ecol. Manage.* 255, 3606–3612.
- Shorohova, E., Ignatyeva, O., Kapitsa, E., Kauhanen, H., Kuznetsov, A., Vanha-Majamaa, I., 2012. Stump decomposition rates after clear-felling with and without prescribed burning in southern and northern boreal forests in Finland. *For. Ecol. Manage.* 263, 74–84.
- Shorohova, E., Kapitsa, E., 2014. Influence of the substrate and ecosystem attributes on the decomposition of coarse woody debris in European boreal forests. *For. Ecol. Manage.* 315, 173–184.
- 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. *For. Ecol. Manage.* 128, 211–225.
- Smolander, A., Heiskanen, J., 2007. Soil N and C transformations in two forest clear-cuts during three years after mounding and inverting. *Can. J. For. Res.* 87, 251–258.
- Smolander, A., Paavola, L., Mäkelä, E., 2000. C and N transformation in forest soil after mounding for regeneration. *For. Ecol. Manage.* 134, 17–28.
- Strukelj, M., Brais, S., Quideau, S.A., Angers, V.A., Kebli, H., Drapeau, P., Oh, S.-W., 2013. Chemical transformations in downed logs and snags of mixed boreal species during decomposition. *Can. J. For. Res.* 43, 785–798.
- van der Wal, A., de Boer, W., Smant, W., van Veen, J.A., 2007. Initial decay of woody fragments in soil is influenced by size, vertical position, nitrogen availability and soil origin. *Plant Soil* 301, 189–201.
- Zell, J., Kändler, G., Hanewinkel, M., 2009. Predicting constant decay rates of coarse woody debris – a meta-analysis approach with mixed model. *Ecol. Model.* 220, 904–912.
- Weedon, J.T., Cornwell, K., Cornelissen, J.H.C., Zanne, A.Y., Wirth, C., Coomes, D., 2009. Global meta-analysis of wood decomposition rates: a role of trait variation among tree species? *Ecol. Lett.* 12, 45–56. <http://dx.doi.org/10.1111/j.1461-0248.2008.01259.x>.
- Yatskov, M., Harmon, M.E., Krankina, O., 2003. A chronosequence of wood decomposition in the boreal forests of Russia. *Can. J. For. Res.* 33, 1211–1226.
- Yin, X., 1999. The decay of forest woody debris: numerical modeling and implications based on some 300 data cases from North America. *Oecologia* 121, 81–98.
- Zhou, L., Dai, L., Gu, H., Zhong, L., 2007. A review on the decomposition and influence factors of coarse woody debris in forest ecosystem. *J. For. Res.* 18, 45–54.