Folia Forestalia Polonica, series A, 2012, Vol. 54 (2), 71–83

ORIGINAL ARTICLE

Carbon and nutrient release during decomposition of coarse woody debris in forest ecosystems of Central Siberia

Liudmila V. Mukhortova

V.N. Sukachev Institute of Forest, Siberian Branch of Russian Academy of Sciences, Akademgorodok, 660036, Krasnoyarsk, Russia, e-mail: l.mukhortova@gmail.com

Abstract

Coarse woody debris (CWD) is often overlooked in studies on the decomposition of organic matter in forest soils. To assess the role of CWD in carbon and nutrient cycling in these forest ecosystems, we investigated changes in carbon and nutrients of differently decomposed CWD samples from the forest tundra and northern, middle, and southern taiga of Central Siberia. Samples included live wood, snags, logs at the classes I, II, and III of decomposition, and fragments of decomposed wood from forest litter.

At northern latitudes CWD released a larger amount of carbon and nutrients during decomposition compared with southern ecosystems, which were characterized by nutrient immobilization and smaller carbon losses from CWD.

We conclude that CWD in northern and southern ecosystems probably plays a different role in biogeochemical cycles. Logs of pine, spruce, and fir in southern ecosystems accumulate significant amount of nutrients in their biomass during decomposition and create relatively nutrient-rich microsites. In contrast, CWD in northern ecosystems appears to be an important source of carbon and nutrient release to the soil solution.

Key words

forest ecosystems, forest-tundra, northern, central and southern taiga, coarse woody debris, decomposition, carbon and nutrients

Introduction

About 73% of boreal forests in the world are situated in Russia, mostly in Siberia (Kuusela 1992; Sokolov 1997). Mature and overripe forests make up about 80% of the total area of Siberia and about 60% of its carbon stock (Sinitsin 1993; Sokolov 1997). These ecosystems contain large amounts of coarse woody debris (CWD). According to Vedrova et al. (2002) the CWD stock of Siberia is almost equal to the litter stock. Furthermore, the amount of CWD can be equal to between 3 and 100% of the amount of live biomass in forest ecosystems (Krankina and Harmon 1995; Shorokhova and Shorokhov 1999).

Dead trees play a number of important roles in the structure and function of ecosystems (Franklin et al. 1987). They provide habitat for a large variety of

Received 2 August 2011 / Accepted 10 April 2012

organisms (Harmon et al. 1986), influence the potential for wild fires (Uhl and Kauffman 1990; Kaufman et al. 1998), and play an important role in the carbon and nutrient cycles (Lambert et al. 1980; Fahey 1983; Krankina and Harmon 1995). In temperate forests CWD is a source of dissolved organic carbon and other solutes, and is an important regulator of nitrogen (N) availability and loss in forests at multiple scales (Hafner and Groffman 2005). Hafner et al. (2005) demonstrated that in temperate forests CWD has a much greater effect than litter on soil solution chemistry.

While on the one hand, decaying logs represent a large stock of carbon and nutrients, on the other hand, they release these components into the soil and atmosphere during decomposition (Spears and Lajtha 2005). As they degrade and become partially buried in soil, they are a source of woody organic soil horizons (de Montigny et al. 1993; Fox et al. 1994). Further, decaying logs are important sites for asymbiotic N fixation (Crawford et al. 1997). According to Ganjegunte et al. (2004), the slow release of nutrients from decaying CWD may help to guard against nutrient loss via leaching and also contribute to a slow-flowing nutrient source for growing trees.

Quantitative information about the elemental and biochemical nature of CWD at different decay stages is necessary for assessing the role of CWD in forest nutrient budgets and nutrient cycling. The objective of this study was to investigate changes in carbon and nutrients in CWD during decomposition in the different climatic conditions present in Central Siberia in order i) assess the role of CWD in carbon and nutrient cycling in forest ecosystems and ii) understand the effects of climate on CWD decomposition patterns.

So far as the main objective of this study was to assess the role of CWD in carbon and nutrient cycling for different natural zones of Central Siberia, we thus analyzed CWD of different tree species in different climatic zones. These tree species are the main forest-forming species for the natural climatic conditions studied, and the main traits of their CWD decomposition determine the role of CWD for these climatic zones.

MATERIAL AND METHODS

Tree boles and logs at different stages of decomposition, as well as fragments of wood from forest litter, were collected from forest ecosystems of different age and stand structures at experimental sites in the Yenisey longitudinal transect established by the International Geosphere-Biosphere (IGBP) Programme (Pleshikov et al. 2002) (Fig. 1). The Yenisey longitudinal transect

Fig. 1. Geographical position of the Yenisey longitudinal transect

stretches over 1,200 km from latitude 70° to 57° north and covers all the natural zones of Central Siberia: the forest tundra, as well as northern, middle, and southern taiga (Pleshikov et al. 2002).

We collected a series of CWD samples, including fresh wood, snags, and logs at three different stages of decomposition, as well as fragments of decomposed wood from forest litter layers. Samples of CWD were collected in larch and spruce forests in the forest tundra zone; in green moss and lichen larch forests in the northern taiga; in pine forests of the green moss and lichen type in the middle taiga; and in pine-fir-spruce stands, and spruce and birch forests of the grass and grass-moss type in the southern taiga zone. Climatic data for studied zones are presented in Tab. 1.

Coarse woody debris was sampled at replicate sample plots located in the different climatic zones of the Yenisey longitudinal transect. In the forest tundra, there were three sample plots (two larch (*Larix gmelinii (Rupr) Rupr.*) with spruce (*Picea obovata Ledeb.*) stands and one spruce with larch stand). In the northern taiga, there were four sample plots (two from lichen larch forests that were 110 and 350 years old, and two from green moss larch forests that were also 110 and 350 years old). In the middle taiga, there were six sample plots with green moss and lichen Scots pine (*Pinus sylvestris L.*) forests of different ages. In the southern taiga, there were six sample plots with spruce (*Picea obovata Ledeb.*), fir (*Abies sibirica Ledeb.*), and birch (*Betula pendula Roth.*) stands. On each of the sample plots, total counting of tree logs was carried out, for each log the decomposition stage was determined, the tree species was identified and samples of CWD were cut out from 8–10 logs that were at various stages of decomposition.

Coarse woody debris was divided into the three decay classes, based on visual and physical properties according to Daniels et al. (1997) and Klimchenko (2005). In this system, the main basis for division is wood density and the presence of bark and branches, as follows:

- Decomposition class I: Wood has not lost its solidity; stems have bark and branches;
- Decomposition class II: Wood has lost some of its solidity; bark easily flakes from wood, but bark and branches are presented on the stems;
- Decomposition class III: Wood has almost fully lost its initial solidity; some bark and large branches remain on the stems).

Woody fragments from the forest litter of the ecosystems studied were also sampled. These wood residues represented the last stage of CWD transformation (decomposition class IV).

The tree species for coniferous CWD was identified for every log or bole at the I and II class of decomposition. Because the studied forest ecosystems are old enough and formed by monodominant or oligodominant tree stands we supposed that CWD at the late decomposition classes is the same coniferous species as the current tree stand. Birch logs differ from other at the all decomposition classes because they have some specificity of decomposition: birch bark remain insignificantly disturbed during the whole period of wood decomposition.

The CWD samples were air-dried. The density of the CWD samples was analyzed by Poluboyarinov's (1976) submergence method (n = 5 – 20).

Tab. 1. Climate characteristics of regions studied

Region	Latitude	MAT, ^{0}C	MAP, mm	ST > 5, °C	ST > 10, °C	RB, kcal	DWP, days
Khantaika (forest-tundra)	69^{0} n.l.	-8,7	463	1109	858	22	60
Nizhniaya Tunguska (northern taiga)	66^{0} n.l.	-6,4	449,5	1175	930	26	130
Zotino (middle taiga)	60^{0} n.l.	-4,5	450	1372	1100	28	185
Bolshaya Murta (southern taiga)	59^{0} n.l.	-3,1	537	1760	1500	35	190

MAT – mean annual temperature; MAP – mean annual precipitation; ST > 5 – sum of temperatures above 5°C; ST > 10 – sum of temperatures above 10°C; RB – radiation balance; DWP – duration of frost-free period.

PRZECINKI?

Chemical analyses were conducted on an average CWD sample for each decay class at each sample plot (wood from logs of the same species and the same decomposition class collected from one sample plot was mixed and used as one sample for chemical analyses). Wood samples of all tree species were analyzed separately. We analyzed larch and spruce CWD in the forest-tundra and northern taiga, pine CWD in the middle taiga, and spruce, fir and birch CWD in the southern taiga zone. Data on chemical composition of coniferous CWD of the same decay status at different sample plots within each of the climatic zones were taken as replicates for statistical analyses. To compare differences in chemical composition between decomposition classes and between the same decomposition classes at different natural zones we used nonparametric Kruskal-Wallis ANOVA and the median test.

Coarse woody debris was ground to a uniform particle size (able to pass through 1 mm mesh), and contents of nutrients: calcium (Ca), magnesium (Mg), potassium (K), and phosphorous (P) were measured by a near-infrared reflectance spectroscopy (PSCO/ICI IBM-PC 4250) analytical system based on Bortsov (2002). Concentrations of carbon and nitrogen in CWD were analyzed by dry combustion using a CNS elemental analyzer (Vario Max, Elementar GmbH, Hanau Germany).

RESULTS

Density of CWD

The density of live wood differed according to the tree species. Larch wood from northern ecosystems had the highest density of all species studied, while the wood of tree species studied in the southern taiga (fir and spruce) had the lowest (Tab. 2). Decomposition of CWD is accompanied by carbon and nutrient release, which consequently reduces wood density. The most significant loss of volume density for CWD was observed in the northern ecosystems where wood lost almost two-thirds of its initial weight during decomposition from live wood to the decomposition class III. Pine logs from the middle taiga lost about half of their initial weight at the decomposition class III. The density of these logs increased after tree death, probably as a result of wood drying. Fir and spruce logs from the southern taiga showed no decrease in wood density at the decomposition classes I–II, and lost only about 26% of their initial weight at the class II–III. The last decomposition class of CWD showed similar densities for all species. It is probable that any further decomposition of CWD would not be accompanied by any significant loss of density.

Table 2. Density of CWD at different climatic zones

Decomposition class	Wood density, g × cm^3		
	Northern taiga	Middle taiga	Southern taiga
Live wood	0.621 ± 0.035	0.459 ± 0.028	0.394 ± 0.026
Class I	0.491 ± 0.031	0.572 ± 0.042	0.374 ± 0.019
Class II	0.319 ± 0.024	0.495 ± 0.030	0.366 ± 0.046
Class III	0.226 ± 0.058	0.260 ± 0.043	0.271 ± 0.061

Depending on the stage of decay of physically intact logs, fragmentation of CWD and subsequent decomposition in the forest litter layer occur. There can also be small changes in the density at this stage due to slow decomposition of residues rich in substances that are resistant to microbial decay (Yatskov et al. 2003).

Concentration of C and nutrients

The total carbon concentration in decomposed CWD represented 460 ± 3.5 to 510 ± 13.0 mg g^{-1} in differently decomposed samples, and this did not change significantly from live wood to wood decomposition class III. A decrease in carbon concentration was observed in litter samples at the stage of wood fragmentation. This decrease amounted to 5–6% in the forest tundra and southern taiga and 1–2% in the northern and middle taiga. Coarse woody debris from the middle and southern taiga showed increasing carbon concentrations of 8–10% during decomposition from live wood to the decomposition class III.

The total nitrogen concentration ranged from 0.10–0.45 mg g^{-1} in live wood to 4.85–8.85 mg g^{-1} in woody fragments. The concentration of N increased according to the decomposition class in all natural zones and for all tree species. The phosphorus concentration ranged from 0.15–0.58 mg g^{-1} in live wood to 0.30–6.99 mg g^{-1} at the decomposition class IV. The concentration of P first decreases after tree death and then rises from the first to the fourth decomposition class Pine logs in the middle taiga had the lowest P concentration in comparison with other species. In pine CWD the P concentration did not exceed 0.3 ± 0.07 mg g^{-1}, even at the last stage of decomposition (class IV).

Calcium concentrations ranged from 2.34–3.82 mg g^{-1} in live wood to 8.82–11.31 mg g^{-1} in woody fragments. Initially, CWD showed a larger Ca concentration in the northern ecosystems than in the southern. During decomposition the Ca concentration gradually increased, finally representing 2.5–4.5 times larger concentration than in live wood. The amount of potassium was 0.3–7.7 mg g^{-1}, and its changes during decomposition did not exhibit any specific tendency. In contrast, magnesium concentrations gradually increased from live wood to woody fragments from the forest floor. At the last decomposition class, CWD contained about 3.5–4.5 times more Mg than live wood.

At all stages of decomposition pine wood from the middle taiga had the smallest P, Ca, and K concentrations.

DISCUSSION

The wood volume density is dependent on tree species (Rabinovich et al. 2001; Yatskov et al. 2003). In our study larch wood at the northern ecosystems initially had the highest volume density in comparison with other tree species growing at the middle and southern taiga.

Carbon concentration in live wood did not differ from north to south but the net C content of CWD was larger for the northern ecosystems because of the higher volume density of live wood in the north (Fig.2). With respect to nutrients, live wood in the northern ecosystems initially contained larger amounts of N, P, Ca, and K. When it came to determining the nutrient level in trees and tree litter, the one dominant factor is species, but climate, the composition of mineral soil, parent material and humus were also of importance (Berg and McClaugherty 2003).

In Central Siberia live wood and CWD in decomposition I class had a very low nitrogen concentration, thus the C-to-N ratio was very high and in many cases exceeded 1,000. The total N concentration in live wood of coniferous species and birch was 0.25–0.70 mg g^{-1} and 1.25 ± 0.08 mg g^{-1}, respectively, and stayed in a similar range to that found by Preston et al. (1998) for Douglas fir, hemlock, and red cedar (from 0.10 to 4.0 g kg^{-1}, depending upon species and decay stage.

In nutrient-poor environments the initial nutrient content of CWD is reported to be a valuable predictor of wood decay (Romero et al. 2005). The chemical composition of wood controls the rate of microbial decomposition. Microorganisms that decompose litter of poor quality (i.e., with low nutrient contents) must utilize nutrients in soil to raise the nutrient content of decomposing material to that of their own mass (Lambert et al. 1980; Zimmerman et al. 1995). Studies in various ecosystems have shown net accumulation of nitrogen during the decomposition of forest-derived litter (Lambert et al. 1980; Robertson & Daniel 1989; Melillo et al. 1983). Nitrogen limits wood-decomposing microorganisms to the decomposition class I (Cowling 1972). Therefore, microorganisms immobilize N during the wood decomposition process, while C is released through respiration (Harmon et al. 1986). As a consequence, the C-to-N ratio declines. Mackensen and Bauhus (2003) proposed using this ratio as an indicator of decomposition stage within a given wood type. Aber & Melillo (1980) suggested using the nitrogen content in combination with the lignin content as a measure of litter quality and, thus, as a predictor of decomposition rates.

Total P concentration in CWD from Central Siberia was significantly larger than that found for CWD from Vancouver Island (Preston et al. 1998), but it was in the same range as that found for CWD from the Netherlands (van Hees 2003) and south-western Alberta (Prescott and Laiho 2002). Just for the middle taiga, P concentration in CWD of the Scots pine in the first three decomposition classes was in the same range as reported by Preston et al. (1998) for this tree species. But the last decomposition stage contained twice as much phosphorus concentration as preceding stages. As is the case of nitrogen, some studies have also reported that the phosphorus content of plant litter decreases during the initial phase and increases slightly during the last stages of decay (Lambert et al. 1980). Preston et al (1998) showed that the concentration of P increased with time in decomposed CWD, especially in the last decomposition class, but Ganjegunte et al. (2004) found that the concentration of P remained the same in log wood throughout the period of decay. In our study P concentration showed a gradual increase only in the middle and southern taiga. Romero et al. (2005) showed that accumulation of phosphorus was lower in the most P-limited areas. A similar trend was shown by Sinsabaugh et al. (1993) in white birch sticks, where low P accumulation occurred in P-limited areas and high P accumulation occurred in areas that were least P-limited.

Potassium is the most mobile mineral element of all the nutrients, and many researchers have shown that K concentration decreases as decomposition progresses (Preston et al. 1998; Krankina et al. 1999; Ganjegunte et al. 2004). In our study we did not observe any gradual decrease in this element. It had different patterns of change during decomposition in different climatic zones, but it was impossible to trace any common tendency in these changes. Moreover, van Hees (2003) found no certain tendency of change in K concentration with decomposition.

Microbial decomposition of wood is accompanied by some mass loss with retention of log volume. This specificity of CWD decomposition allows to trace net changes of mass of an element independently of other elements, if this is calculated at the unit of volume (mg cm^{-3}) in contract to the concentration that is estimated as relative amount in the unit of weight (mg g^{-1}). Net mass of an element in the volume unit is calculated as multiplication of its concentration (mg g^{-1}) by the wood volume density (g cm^{-3}).

If the decrease in volume density during decomposition of CWD is taken into account, then a significant decrease in carbon content during decomposition can be calculated (Fig. 3). From decomposition classes I–III, wood loses 25–64% of its initial C. Initial carbon content in live wood gradually decreases from north to south, something that is mainly related to differences in wood density. During decomposition the most significant loss of carbon was observed for CWD from the northern ecosystems (64% of total initial carbon content); loss gradually decreased toward the middle taiga (40%), and then toward the southern taiga (25% of initial carbon content). In contrast, net immobilization of N of between 0.141 and 0.450 mg N cm^{-3} occurred in different climatic zones (Fig.3).

Krankina et al. (1999) measured the concentration of 12 nutrients in decaying logs of Scots pine, Norway spruce, and birch in northwest Russia. They found nearly all nutrients showing an increase in concentration as logs passed through decay classes III, IV. The exception was K and boron (B). Although the concentration of many of the elements increased, there was no net accumulation of nutrients over the course of decay, except for aluminium (Al) and sodium (Na). In our study different patterns of changes in net nutrient content during decomposition were found in different natural zones:

- CWD in the forest-tundra forests lost all nutrients during decomposition;
- CWD in the northern taiga lost only K, Mg, and P, but significantly accumulated Ca;
- CWD in the middle taiga differed with respect to accumulation of Ca, K, and Mg and retention of P in biomass during decomposition;
- Decomposed logs in the southern taiga lost only K during decomposition.

Similar patterns of nutrient dynamics have been reported by other authors. Sollins et al. (1987) docu-

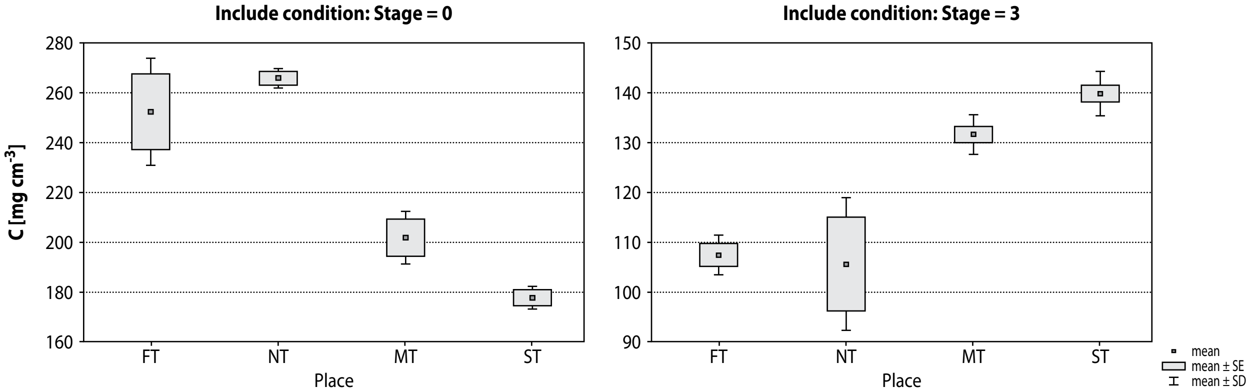
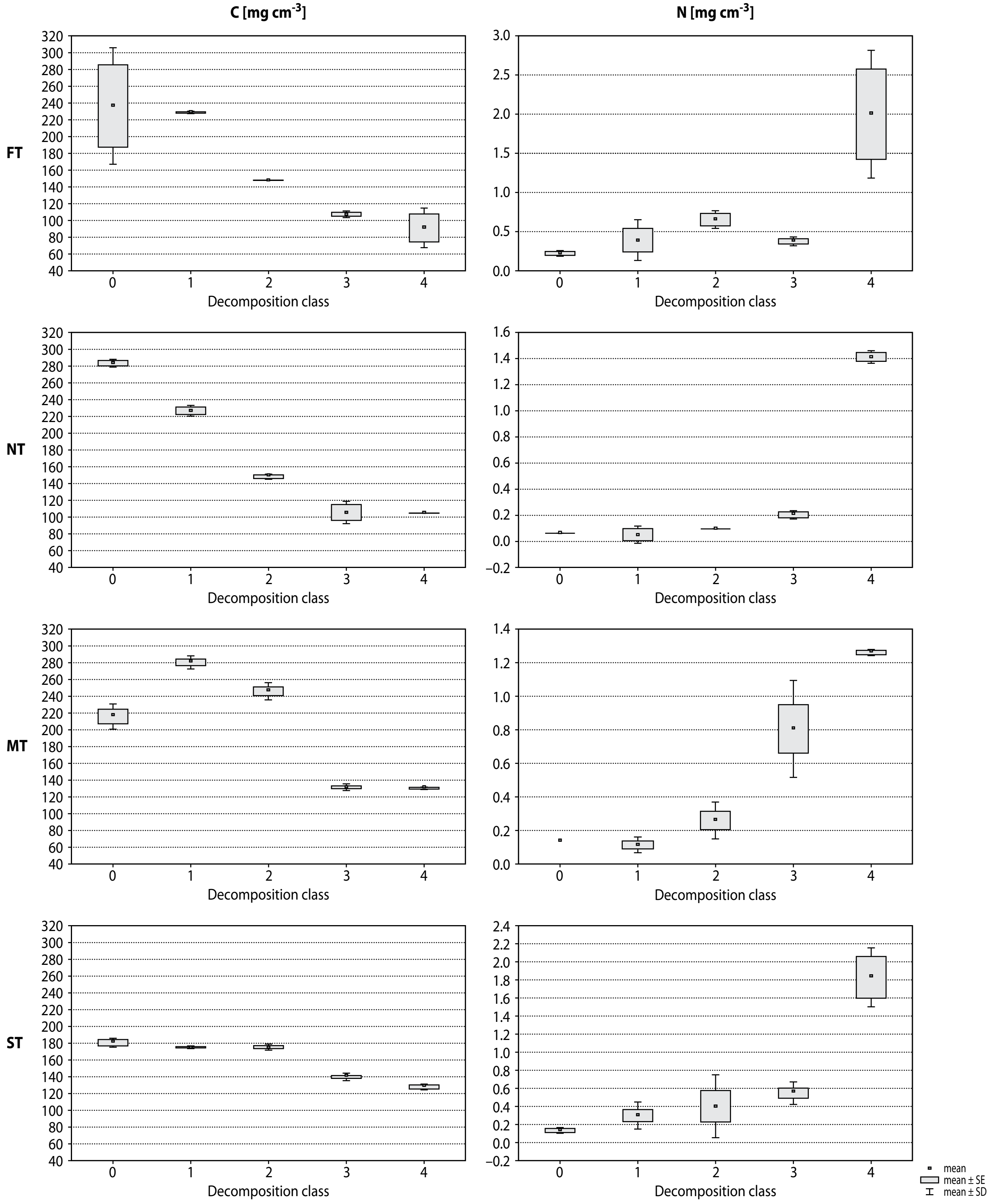
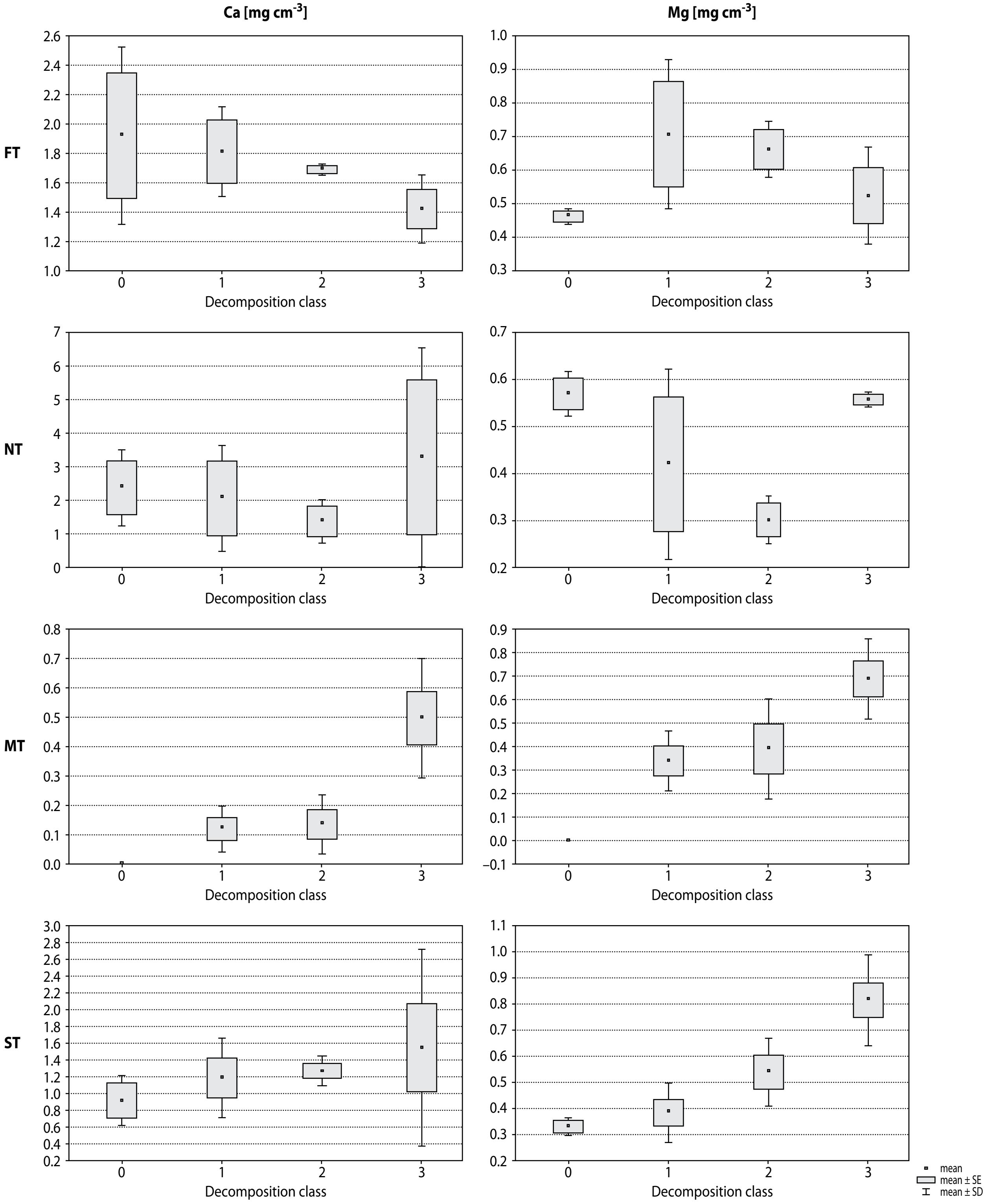


Fig. 2. Carbon content (mg cm^{-3}) in live wood (include condition: Stage = 0) and in CWD of III decomposition class (include condition: Stage = 3) in studied natural zones: FT – forest-tundra; NT- northern taiga; MT – middle taiga; ST – southern taiga


C [mg cm-3]
N [mg cm-3]
FT
NT
MT
ST
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
−0.2
2.4
2.2
1.8
0
1
2
3
4
Decomposition class
mean
mean ± SE
mean ± SD


Ca [mg cm^{-3}]
Mg [mg cm^{-3}]
FT
NT
MT
ST
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
–0.1
7
6
5
4
3
2
1
0
3.0
2.8
1.1
0
1
2
3
Decomposition class
mean
mean ± SE
mean ± SD

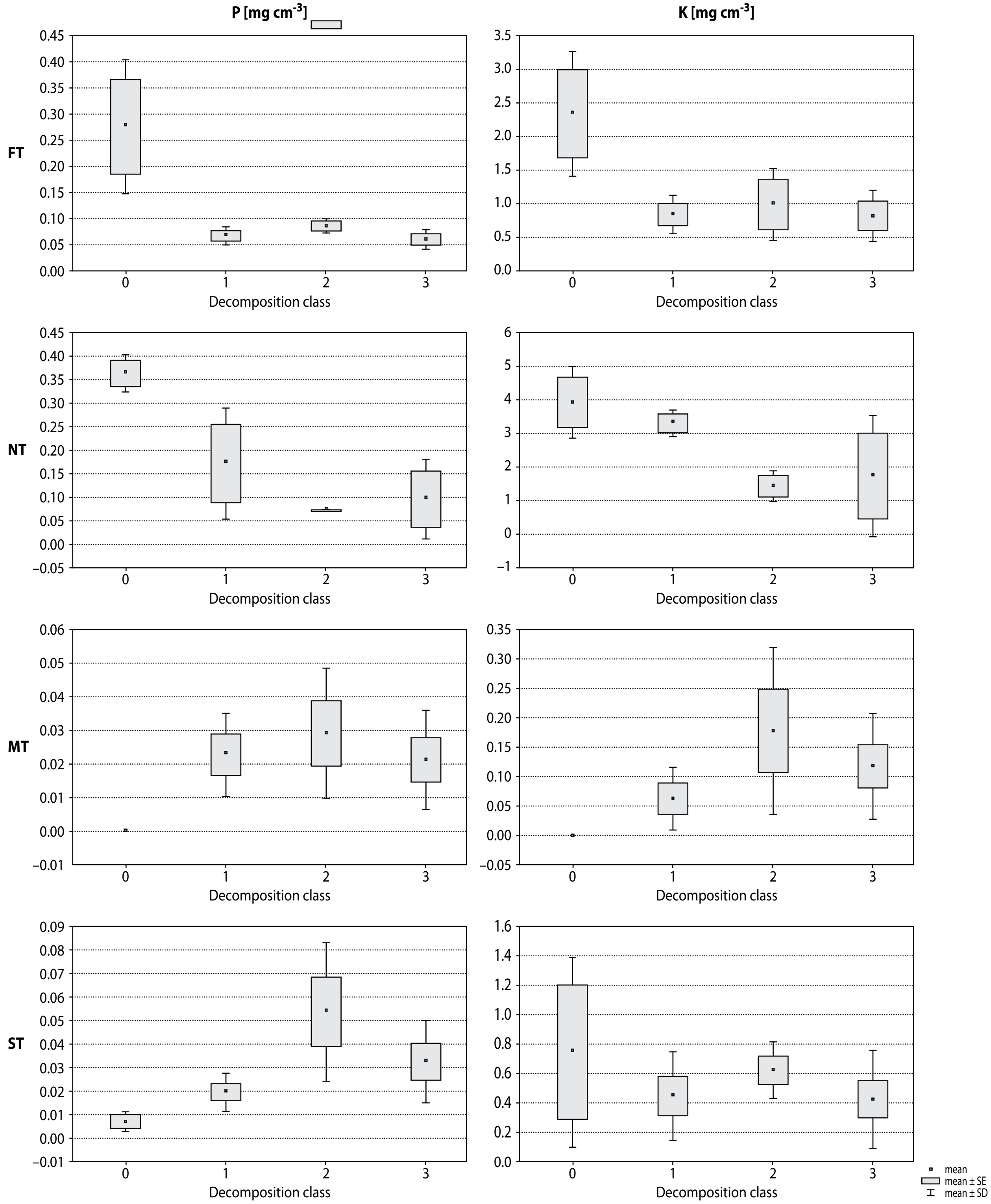


Fig. 3. Changes in patterns of net carbon (C, mg cm^{-3}) and nutrients (N, Ca, Mg, P, K, mg cm^{-3}) content during CWD decomposition in different natural zones: FT- forest-tundra; NT- northern taiga; MT – middle taiga; ST – southern taiga. X-coordinates: 0 – live wood; 1 – I decomposition class; 2 – II decomposition class; 3 – III decomposition class; 4 – IV decomposition class

mented net gains in N, P, and Mg per unit volume of Douglas fir logs. Busse (1994) studied decomposition of lodgepole pine wood and noted net losses of Ca, Mg, and K, but with P remaining constant.

Harmon et al. (1994) found that fungi can accumulate 38–136 times more N, P, and K than the logs on which they are growing. This enrichment occurs largely through mycelial transport out of the log and the surrounding environment into the sporocarp.

The live wood of forest-forming species in the north is richer in nutrients (with the exception of N) than the wood of trees growing more to the south. During decomposition, this difference decreases because of nutrient release from CWD in the northern ecosystems and nutrient immobilization in CWD in the middle and southern taiga (Fig. 3). This is mainly related to different demands on the part of the main decomposer species at work in these climatic conditions and/or because of decomposing wood in these zones is from different tree species.

The role of Ca and manganese (Mn) in decomposition has largely been overlooked in the ecological literature. The specific roles of Ca in the degradation of phenolic substructures of the lignin component of wood have been identified and reported in the plant pathology and wood chemistry literature (e.g. Forrester et al. 1988; Hammel 1997; Paszczyński et al. 1985). However, there is no information about a role of Mg in wood decomposition, although net gain in Mg content has been noted by many researchers (Sollins et al. 1987; Means et al. 1992).

Carbon concentration in CWD indicates different patterns of change during decomposition in different climatic zones. In the northern taiga, especially in the forest-tundra zones, carbon concentration decreased during decomposition, while in the middle and southern taiga significant increases in C concentrations were observed. It may be a result of different patterns of lignin and carbohydrate decomposition in CWD in the northern and southern ecosystems.

The main microorganisms active in wood decomposition in boreal forests are fungi (Tarasov 2002). Wood decay by fungi is usually classified into three types: soft rot, brown rot and white rot. A series of cellulolytic enzymes are employed in the degradation process by brown rot fungi, but no lignin degrading enzymes are typically involved. White rot fungi possess both cellulolytic and lignin degrading enzymes and these fungi, therefore, have the potential to degrade the entirety of the wood structure under sufficient environmental conditions. Soft rot fungi typically attack higher moisture and lower lignin content wood, and can create unique cavities in the wood cell wall (Goodell et al. 2008). Many studies have demonstrated that the lignin-rich residues remaining after brown-rot decay can be enriched in metals, particularly Ca, iron (Fe), Mn and Mg (Ostrofsky et al. 1997; Jellison et al. 1997). One of the key differences between brown-rot decay fungi and white-rot decay fungi is the accumulation of oxalic acid during decomposition by brown-rot fungi (Green et al. 1991; Dutton and Evans 1996). Because they product oxalate decarboxylase, most white-rot fungi degrade oxalic acid, while brown-rot fungi accumulate this organic acid driving the pH of the microenvironment below 2.0. Oxalate in the solution can increase effective solubility of cations (as shown for Al and Fe) in soil, increasing the transport of these ions into wood during brown-rot decay (Griffiths et al. 1994).

Based on the results of the analysis of chemical composition of CWD and on our visual observations, we make a conjecture that the main wood-decaying microorganisms on CWD in the northern ecosystems can be white-rot fungi, and in the southern ecosystems -brown-rot fungi. This supposed difference of decomposer complexes was put forward by Berg and McClaugherty (2003). They proposed that under less-limiting climatic conditions, faster-growing brown rot fungi have an advantage over slower-growing white rot fungi. In colder climates lignin degraders would grow relatively better than fungi that degrade holocellulose.

CONCLUSION

The patterns of CWD decomposition for the northern and southern ecosystems differ substantially. The decomposition of CWD at northern latitudes results in larger losses of carbon and nutrients for the duration of decomposition classes I–III, while the more southern ecosystems are characterized by immobilization of nutrients (Ca, Mg) from the surrounding areas or conservation of nutrients (P, K) in CWD.

The extent to which CWD influences the biogeochemical processes of its surroundings is controlled by many factors including CWD's original chemical and structural composition and, in no small part, the nature of chemical alteration imparted to it during microbial degradation. Thus, it seems that CWD in northern and southern ecosystems plays different roles in biogeochemical cycles. Logs of pine, spruce, and fir in the southern ecosystems accumulate a significant amount of nutrients in their biomass during decomposition and create relatively nutrient-rich microsites. In contrast, CWD of larch and spruce in the northern ecosystems are probably a source of nutrient release to soil and groundwater. The main reason for such differences is probably the different decomposition processes occurring in these zones, which are connected to the specificity of microbial complexes decaying wood in these conditions.

ACKNOWLEDGMENTS

The authors gratefully acknowledge financial support for this research from the German Academic Exchange Service (DAAD) (grant № A/05/05326), Russian Fund for Basic Research (RFBR) (projects № 10–04–00337, № 11–04–01884, and № 11–04–98008 and №11–04–98089).

REFERENCES

Aber J.D., Melillo J.M. 1980. Litter decomposition: measuring relative contributions of organic matter and nitrogen of forest soils. *Canadian Journal of Botany*, 58, 416–421.

Berg B., McClaugherty Ch. 2003. Plant litter: decomposition, humus formation, carbon sequestration. Springer-Verlag, Berlin, pp. 286.

Bortsov V.S. 2002. Using of automatized analytical system on base of catoptric spectroscopy in agrocoenoses researches. Abstract of PhD thesis. Krasnoyarsk State Agrarian University, Krasnoyarsk, pp. 18.

Busse M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of Central Oregon. *Soil Science Society of American Journal,* 58 (1), 221–227.

Cowling E.B. 1970. Nitrogen in forest trees and its role in wood deterioration. Abstracts of Uppsala Dissertations in Science, 164.

Crawford R.H., Li C.Y., Floyd M. 1997. Nitrogen fixation in root-colonized large woody residues of Oregon coastal forests. *Forest Ecology and Management,* 92, 229–234.

Daniels L.D., Dobry J., Klinka K., Feller M.S. 1997. Determining year of death of logs and snags of Tuja plicata in sowthwestern coastal British Columbia. *Canadian Journal of Forest Research*, 27, 1132–1141.

De Montigny L.E., Preston C.M., Hatcher P.G., Kogel-Knabner I. 1993. Comparison of humus horizons from two ecosystem phases on northern Vancouver Island using 13C-CPMAS-NMR spectroscopy and CuO oxidation. *Canadian Journal of Soil Science*, 73, 9–25.

Dutton M.V., Evans C.S. 1996. Oxalate production by fungi: its role in pathogenicity and ecology in the soil environment. *Canadian Journal of Microbiology*, 42, 881–895.

Fahey T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta ssp. latifolia*) ecosystems, southeastern Wyoming. *Ecological Monographs*, 53, 51–72.

Forrester I.T., Grabski C.G., Burgess R.R., Leatham G.F. 1988. Manganese, Mn-dependent peroxidases, and the biodegradation of lignin. *Biochemical and Biophysical Research Communications*, 157, 992–999.

Fox C.A., Preston C.M., Fyle C.A. 1994. Micromorphological and 13C-NMR characterization of a humic, lignic and hastic folisol from British Columbia. *Canadian Journal of Soil Science*, 74, 1–15.

Franklin J.F., Shugart H.H., Harmon M.E. 1987. Tree death as an ecological process. *BioScience*, 37, 550–556.

Ganjegunte G.K., Condron L.M., Clinton P.W., Davis M.R., Mahieu N. 2004. Decomposition and nutrient release from radiate pine (*Pinus radiata*) coarse woody debris. *Forest Ecology and Management*, 187, 197–211.

Goodell B., Qian Y., Jellison J. 2008. Fungal decay of wood: soft rot—brown rot—white rot. In: Development of commercial wood preservatives (eds.: T.P. Schultz, H. Militz, M.H. Freeman, B. Goodell, D.D. Nicholas). ACS Symposium Series, Vol. 982, 9–31.

Green F., Larsen M.J., Winandy J.E., Highley T.L. 1991. Role of oxalic acid in incipient brown-rot decay. *Material und Organismen*, 26, 191–213.

Griffits R.P., Baham J.E., Caldwell B.A. 1994. Soil solution chemistry of ectomycorrhisal mats in forest soil. *Soil Biology and Biochemistry*, 26 (3), 331–337.

Hafner S., Groffman P.M. 2005. Soil nitrogen cycling under litter and coarse woody debris in a mixed forest in New York State. *Soil Biology and Biochemistry*, 37, 2159–2162.

Hafner S.D., Groffman P.M., Mitchell M.J. 2005. Leaching of dissolved organic carbon, dissolved organic nitrogen, and other solutes from coarse woody debris and litter in a mixed forest in New York State. *Biogeochemistry*, 74, 257–282.

Hammel K.E. 1997. Fungal degradation of lignin. In: Driven by nature: Plant litter quality and decomposition (eds.: G. Gadish, K.E. Giller). CAB International, Wallingford, U.K., 33–45

Harmon M.E., Franklin J.F., Swanson F.J. et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, 15, 133–302.

Harmon M.E., Sexton J., Caldwell B.A., Carpenter S.E. 1994. Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P and Zn from conifer logs in the early stages of decomposition. *Canadian Journal of Forest Research*, 24, 1883–1893.

Jellison J., Conolly J., Goodell B., Doyle B., Illman B., Fekete F., Ostrofsky A. 1997. The role of cations in the biodegradation of wood by the brown rot fungi. *International Biodeterrioration and Biodegradation*, 39, 165–179.

Kaufman J.B., Cummings D.L., Ward D.E. 1998. Fire in the Brazilian Amazon. 2. Biomass, nutrient pools and losses in cattle pasture. *Oecologia*, 113, 415–427.

Klimchenko A.V. 2005. Carbon accumulation in logs of larch forests in Northern taiga of Central Siberia. *Lesnoe hoziaystvo,* 5, 33–34.

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.K., 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. *Canadian Journal of Forest Research*, 29, 20–32.

Kuusela K. 1992. Boreal forestry in Finland: a fire ecology without fire. *Unasylva*, 43 (170), 20–25.

Lambert R.L., Lang G.E., Reiners W.A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology*, 61, 1460–1473.

Mackensen J., Bauhus J. 2003. Density loss and respiration rates in coarse woody debris of *Pinus radiate, Eucaliptus regnans* and *Eucaliptus maculate*. *Soil Biology and Biochemistry*, 35, 177–186.

Means J.E., MacMillan P.C., Cromack K.Jr. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, U.S.A. *Canadian Journal of Forest Research*, 22, 1536–1546.

Melillo J.M., Naiman R.J., Aber J.D., Eshleman K.N. 1983. The influence of substrate quality and stream size on wood decomposition dynamics. *Oecologia*, 38, 281–285.

Ostrofsky A., Jellison J., Smith K.T., Shortle W.C. 1997. Changes in cation concentrations in red spruce wood decayed by brown rot and white rot fungi. *Canadian Journal of Forest Research*, 27, 567–571.

Paszczyński A., Huynh V.B., Crawford R. 1985. Enzymatic activities of an extracellular, manganese-dependent peroxidase from *Phanerochaete chrysosporum*. *FEMS Microbiology Letters*, 29, 37–41.

Pleshikov F.I., Vaganov E.A., Vedrova E.F. et al. 2002. Forest ecosystems of the Yenisey meridian. (in Russian) Publishing House of SB RAS, Novosibirsk, pp. 356.

Poluboyarinov O.I. 1976. Wood density. Lesnaya promishlennost’, Moscow, pp. 200.

Prescott C.E., Laiho R. 2002. The nutritional significance of coarse woody debris in three Rocky Mountain coniferous forests. *USDA Forest Service General Technical Reports*, PSW-GTR-181, 381–392.

Preston C.M., Trofymov J.A., Niu J., Fyfe C.A. 1998. 13CPMAS- NMR spectroscopy and chemical analysis of coarse woody debris in coastal forests of Vancouver Island. *Forest Ecology and Management*, 111, 51–68.

Rabinovich M.L., Bolibova A.V., Kondrashenko V.I. 2001. Theoretical basis of biotechnology of woody composites. I. Wood and decomposed it fungi. Nauka, pp. 320.

Robertson A.I., Daniel P.A. 1989. Decomposition and the annual flux of detritus from fallen timber in tropical mangrove forests. *Limnology and Oceanography*, 34, 640–646.

Romero L.M., Smith T.J., Fourqurean J.W. 2005. Changes in mass and nutrient content of wood during decomposition in a south Florida mangrove forest. *Journal of Ecology*, 93, 618–631.

Shorohova E.V., Shorohov A.A. 1999. Characteristics of detritus decay classes for spruce, birch, and aspen in middle taiga spruce forests. St. Petersburg Forestry Research Institute Publishers, St. Petersburg, pp. 210.

Sinitsin S.G. 1993. Effective use the forests of Russia under the solving of ecological problems of world community. *Lesnoe Hoziaystvo*, 5, 1–7.

Sinsabaugh R.L., Antibus R.K., Linkins A.E., McClaugherty C.A., Rayburn L., Repert D. et al. 1993. Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. *Ecology*, 74, 1586–1593.

Sokolov V.A. 1997. Fundamentals to forest management in Siberia. SB RAN, Krasnoyarsk, pp. 308.

Sollins P., Cline S.P., Verhoeven T., Sachs D., Spycher G. 1987. Patterns of log decay in old- growth Douglas-fir forests. *Canadian Journal of Forest Research,* 17, 1585–1595.

Spears J.D.H., Lajtha K. 2005. The imprint of coarse woody debris on soil chemistry in the Western Oregone Cascades. *Biogeochemistry*, 71 (2), 163–175.

Tarasov M.E. 2002. Methodical approaches to estimation of wood detritus decomposition rate. *Lesovedenie*, 5, 32–38.

Uhl C., Kaufman J.B. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology*, 7, 437–449.

Van Hees A.F.M. 2003. Decay and Physical-chemical Characteristics of Dead Beech Wood in The Netherlands. NAT_MAN Working Report 45.

Vedrova E.F., Stakanov V.D., Pleshikov F.I. 2002. Regularity of carbon pool changes in boreal forests. (in Russian) In: Forest ecosystems of the Yenisey meridian. (ed.: F.I. Pleshikov). Publishing House of SB RAS, Novosibirsk, 206–221.

Yatskov M., Harmon M.E., Krankina O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. *Canadian Journal of Forest Research*, 33, 1211–1226.

Zimmerman W.M., Pulliam W.D., Lodge D.J., Quinones-Orfila V., Fetcher N., Guzman-Grajales S. et al. 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. *Oikos*, 72, 314–322.