

**This is an electronic reprint of the original article.
This reprint *may differ* from the original in pagination and typographic detail.**

Author(s): Nieminen, Jouni; Pohjola, Pekka

Title: Labile carbon addition affects soil organisms and N availability but not cellulose decomposition in clear-cut Norway spruce forests

Year: 2014

Version:

Please cite the original version:

Nieminen, J., & Pohjola, P. (2014). Labile carbon addition affects soil organisms and N availability but not cellulose decomposition in clear-cut Norway spruce forests. *Boreal Environment Research*, 19(4), 257-266.
<http://www.borenv.net/BER/pdfs/ber19/ber19-257.pdf>

All material supplied via JYX is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the repository collections is not permitted, except that material may be duplicated by you for your research use or educational purposes in electronic or print form. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone who is not an authorised user.

Labile carbon addition affects soil organisms and N availability but not cellulose decomposition in clear-cut Norway spruce forests

Jouni K. Nieminen¹⁾ and Pekka Pohjola²⁾

¹⁾ Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland (e-mail: jouni.k.nieminen@elisanet.fi)

²⁾ Biodeg Finland, Orivedentie 5, FI-17800 Kuhmoinen, Finland

Received 23 Oct. 2012, final version received 18 Aug. 2013, accepted 19 Aug. 2013

Nieminen, J. K. & Pohjola, P. 2014: Labile carbon addition affects soil organisms and N availability but not cellulose decomposition in clear-cut Norway spruce forests. *Boreal Env. Res.* 19: 257–266.

We assessed the effects of sucrose addition on the biological and chemical properties of organic soil in clear-cut Norway spruce forests managed with or without wood-ash fertilization and mechanical site preparation. Sucrose addition increased the abundances of enchytraeids and tardigrades and soil moisture percentage in the clear-cut areas. Sucrose also increased nematode abundance in the non-fertilized plots. Sucrose reduced the pool of water-extractable $\text{NH}_4\text{-N}$ in the soil in the first year, but increased it in the second year. Sucrose addition did not affect the decomposition rate of cellulose strips. The biomass of ground vegetation was not affected by sucrose. Carbohydrate addition seems to enhance N immobilization in clear-cut areas in the short term, and it is suggested that aims at reducing N loss from disturbed forest soil do not necessarily accelerate carbon loss from the forest ecosystem.

Introduction

Management practices such as clear-cutting, mechanical site preparation and fertilization can disturb the structure and functioning of soil food webs in forest ecosystems (Bormann *et al.* 1968, Aronsson and Ekelund 2004, Chatterjee *et al.* 2008). Disturbances can alter the resources of soil organisms directly by increasing nutrient import or export (Hyvönen *et al.* 2007) and indirectly, by modifying chemical and physical properties of the forest floor, such as pH, temperature, moisture and aeration (For example Keenan and Kimmins 1993). Here we focus on the question of enhancing nitrogen immobilization in the soil food web without increasing the loss of soil organic carbon.

Clear-cutting alters the quality and quantity of carbon (C) resources available in the forest floor (Smolander *et al.* 2001, Hannam *et al.* 2005), and leads to C emissions to the atmosphere (Howard *et al.* 2004). Less carbon is available to decomposers in managed forests now when an increasing proportion of logging residues such as branches, tree tops and stumps is used as fuel (Rudolph and Gustafsson 2005). Most of the C resources in logging residues are not immediately available to decomposers even when masticated and incorporated in soil (Busse *et al.* 2009). In contrast, roots and root exudates (Pollierer *et al.* 2007), canopy leaching and honeydew excreted by aphids (Stadler and Michalzik 1998) provide soil food webs with readily usable C compounds. Thus, the reduction of labile C availability caused

by tree removal can be more important to decomposer food webs than harvesting of logging residues in the short term. For example, clear-cutting reduced microbial biomass and respiration (Siira-Pietikäinen *et al.* 2001, Lindo and Visser 2003) and nematode abundance (Sohlenius 1982) temporarily after the harvest.

In parallel with changes in the availability of easily decomposable carbohydrates, management practices can also disrupt N dynamics in forest ecosystems (Bormann *et al.* 1968). Fungal:bacterial (F:B) ratio and gross mineralization rate are negatively associated in forest ecosystems because ectomycorrhizal fungi are an important nutrient sink (Högberg *et al.* 2007). Disturbed ecosystems are often characterized by reduced F:B ratios (Bååth *et al.* 1995) and increased net N mineralization (Smolander *et al.* 2001, Nieminen 2008a). Clear-cutting and mechanical site preparation can enhance N mineralization from organic soil layer (Dahlgren and Driscoll 1994, Lindo and Visser 2003, Nieminen *et al.* 2012). On the other hand, plant biomass is low in the first years after clear-cutting. Thus, more inorganic N may become available than can be taken up by the ground vegetation and planted tree seedlings. Nitrification of excess $\text{NH}_4\text{-N}$ can increase N leaching from the forest ecosystem (Dahlgren and Driscoll 1994, Schmidt *et al.* 1996, Smolander *et al.* 2001), which in turn can cause eutrophication of adjacent lakes and streams (Smith *et al.* 1999).

Addition of organic material whose C:N ratio is high — such as logging residues (O'Connell *et al.* 2004, Homyak *et al.* 2008, Busse *et al.* 2009) or paper mill sludge (Young *et al.* 1993, Feldkirchner *et al.* 2003) — has been suggested as means to decrease N loss from forest ecosystems. Organic amendment of high C:N could ease the C limitation of decomposer growth and hence enhance immobilization of N in microbial biomass. A high resource C:N ratio can increase the F:B ratio in some situations (Bossuyt *et al.* 2001) but this has not always been found in clear-cut areas (Busse *et al.* 2009).

Labile carbon can stimulate the decomposition of more recalcitrant soil organic matter (SOM) (“positive priming effect”, Kuzyakov *et al.* 2000, Fontaine *et al.* 2007). Ekblad and Högberg (2000) found no evidence of positive priming in the humus layer of boreal forest

soil. Climate change mitigation requires that measures aimed at retaining N in the forest ecosystem should not increase C emissions to the atmosphere. There is thus a need to consider the longer-term ecosystem-level effects of labile C in disturbed forest ecosystems.

Enchytraeids and bacterial-feeding nematodes were our main target organisms. One enchytraeid species, *Cognettia sphagnetorum* has a high biomass, and affects nutrient cycling and plant growth. For example, Setälä (2000) showed that *C. sphagnetorum* alone stimulated pine growth as much as a diverse soil animal community. This has lead soil ecologists to call *C. sphagnetorum* “a keystone species” in boreal forest soil. Bacterial-feeding nematodes were chosen because they can be used as indicators of the dominance of either bacterial- or fungal-based food chain (Sánchez-Moreno *et al.* 2006).

We investigated the interactive effects of sucrose addition, wood-ash fertilization and mechanical site preparation on the biological and chemical properties of the humus layer at two clear-cut Norway spruce forests. We hypothesized that sucrose addition increases the biomass of key components of the soil food web, such as enchytraeids and nematodes, in the first growing seasons after clear-cutting. A single carbohydrate input was expected to have only transient effects on the soil food web. We expected that carbohydrate addition on the soil surface would attract sugar fungi, the spores of which disperse effectively through the air. Thus, we hypothesized that sucrose addition would favour fungal-based food chains (Bossuyt *et al.* 2001), or in other words, reduce the proportion of bacterial-feeding nematodes. No effect of sucrose addition on the decomposition rate of cellulose was expected. Finally, we hypothesized that more N would be immobilized in the soil food web, and as a consequence, the pools of water-extractable N would be smaller in sucrose amended plots in the first years after clear-cutting.

Material and methods

Study sites and experimental design

The experiment was established at the end of

June 2009 in two Norway spruce forests situated ca. 100 km apart, one in Viitasaari (63°14'N, 26°5'E) and another in Ähtäri (62°43'N, 24°18'E), central Finland, both clear-cut in the previous winter. The soil type is Haplic podzol. The biological, physical and chemical properties of the sites are described in Nieminen *et al.* (2012) (*see* also Table 1).

The experimental area at both sites was divided into 3 blocks (15 × 15 m each; hereafter referred to as “block”). Norway spruce seedlings were planted in each block in a regular grid using planting devices M-Planter and Bräcke, both of which employ the spot-mounding method. In the spot-mounding method, a patch of soil is turned upside down onto the adjacent intact forest floor and the tree seedling is planted in the highest part of the mound (Saarinen 2006). Thus, a typical mound consists of a variable amount of mineral soil on top of a two-fold humus layer. Half of the seedlings were planted with and the rest without spot mounding. Half of the seedlings on mounded and intact forest floor were fertilized by adding granulated wood ash (314 g per plot, equalling 4 Mg ha⁻¹) uniformly to circular tree-centred plots (diam. 1 m; hereafter referred to as “plot”). Each experimental plot was thus subjected to one of the four possible combinations of site preparation and fertilization: control (no spot mounding, no wood ash addition), spot mounding, wood ash, spot mounding and wood ash. The effects of spot mounding and wood ash on the biological and chemical properties of organic soil layer have been reported elsewhere

(Nieminen *et al.* 2012). Here we focus on the effects of carbohydrate addition.

Solid sucrose (262 g per plot, equalling 1 Mg C ha⁻¹) was added to half of the plots immediately after planting. Each of the eight treatment combinations was replicated three times in each block. The total number of seedlings in the experiment was 144 (2 sites × 3 blocks × 3 treatments × 2 levels × 3 replicates).

The ash consisted of granulated mixed-wood and peat (< 20%) ash, hereafter called “wood ash”, initially containing 200 g kg⁻¹ calcium (Ca), 22 g kg⁻¹ potassium (K) and 11 g kg⁻¹ phosphorus (P), 10 mg kg⁻¹ cadmium (Cd) and 20 mg kg⁻¹ arsenic (As), and 13% water.

Sampling

There were two similar samplings in all plots, the first in September 2009 and the second in September 2010. In each plot, the following cores were taken with a steel corer from the organic soil layer: one for enchytraeid and another for microarthropod extraction (57 mm diam., 4–5 cm deep), and one (35 mm diam.) for nematode extraction and physico-chemical determinations. Only the top-most organic layer was sampled in the mounded plots. All ash granules found in the samples were removed. Soil cores were put in separate plastic bags and transported in cooled polystyrene boxes to the laboratory where each core was weighed to estimate its fresh mass. Before extraction, the samples were stored at 0–5 °C.

Table 1. Initial physical, chemical and biological properties of organic soil layer (mean ± SE) in clear-cut Norway spruce forests in Ähtäri and Viitasaari. Significant test results are given in boldface.

	Ähtäri	Viitasaari	Site effects ^a	
			<i>t</i>	<i>p</i>
Humus layer depth (mm)	41 ± 4	55 ± 5	-1.9	0.078
pH (H ₂ O)	4.37 ± 0.02	4.36 ± 0.06	-0.01	n.s.
Soil moisture (% OM)	280 ± 11	305 ± 14	-2.86	0.007
Organic matter content (%)	60 ± 5	67 ± 7	-0.47	0.64
Total water-extractable N (μg g _{om} ⁻¹)	54 ± 10	76 ± 16	-2.0	0.05
Total water-extractable N (kg ha ⁻¹)	3.1 ± 0.7	5.3 ± 1.1	-2.5	0.015
Proportion of bacteria-feeding nematodes (%)	74 ± 5	75 ± 5	-1.0	0.33
Enchytraeid abundance (indiv. g _{om} ⁻¹)	3 ± 0.6	7 ± 1	-2.6	0.01

^a The initial properties of the two sites were compared using Student's *t*-test; df = 48 except for humus layer depth for which df = 11.

Above-ground plant biomass was harvested from a 0.25 m² area surrounding the seedlings within each plot in July. After the higher plants were identified the vegetation samples were oven-dried (+ 40 °C) and weighed.

Subsamples of the soil cores were weighed, oven-dried (105 °C) for 24 hours, cooled in a desiccator, and weighed again. Soil organic matter content (1 – ash mass/dry mass) was measured on a loss-on-ignition basis (4 h at 550 °C). Moisture percentage on an ash-free basis as $100 \times (fm - dm)/(om \text{ content} \times dm)$, where fm and dm denote fresh and dry mass, respectively.

Soil animals

Enchytraeids were extracted from about 20 g of fresh soil for 4 h with heating and nematodes from about 3 g fresh soil for 24 h without heating using the Baermann wet funnel technique (O'Connor 1957). Microarthropods were extracted for ca. one week from the soil cores with a computer-controlled high-gradient extractor (dry funnels).

Collembolans and mites were enumerated on preserved samples. Living enchytraeids, nematodes and tardigrades were counted after the extraction and animal abundances were expressed as number of individuals per g of soil organic matter. The biomasses of enchytraeid populations were calculated as described in Nieminen (2009a).

A subset of nematodes in each sample was classified as bacterial-feeders, predators or others (fungal-feeders, herbivores and omnivores) using Yeates *et al.* (1993) and the proportions of these groups were expressed as percentages of total nematode abundance.

Cellulose decomposition

We used cellulose strips to assess decomposition activity in the clear-cut areas, because the mass loss rate of cellulose strips is strongly correlated with that of local needle litter in boreal forest soil (Kurka 2001). In each plot belonging to Mounding and Sucrose treatments, one nylon

mesh bag (65 × 130 mm, mesh size 1 mm) containing three weighed cellulose strips in separate compartments was buried in the topsoil (ca. 1 cm depth). The initial mass and the ash content of the cellulose strips were 1.07 ± 0.03 g, and $6\% \pm 0.7\%$ (mean ± SD, $n = 5$), respectively.

One cellulose strip was removed from each mesh bag at each sampling. The cellulose strips were oven dried (65 °C), weighed, and their final organic matter content was assessed on the basis of loss-on-ignition (4 h at 550 °C).

Chemical analyses

To estimate the size of the soluble NH₄-N-pool, the water-extractable NH₄-N was extracted by soaking 5 g (fm) soil overnight in 50 ml of distilled deionized water. The extracts were filtered through 1.6 μm glass microfibre filters (Whatman no. 1822055) and 0.45 μm membrane filters (Supor 450 Membrane 61854, Pall Corporation 600 South Wagner Road, Ann Arbor, Michigan), stored at –20 °C, and analyzed for pH, conductivity and water extractable NH₄-N according to the standard SFS-EN ISO 11732:2005. NH₄-N concentration of the extract, c_N (mg l⁻¹), was converted into soil N concentration (μg g⁻¹ om) and further to pool size (kg ha⁻¹) using the fresh mass, moisture and organic matter content of the soil samples and the corer size as follows:

$$N (\mu\text{g g}^{-1} \text{ om}) = [(50 + (1 - dm) \times 5) / (dm \times om \times 1000 \times 5)] c_N \quad (1)$$

$$N (\text{kg ha}^{-1}) = 3.785 \times 10^{-3} \times (\text{sample fm}) \times dm \times om \times N (\mu\text{g g}_{\text{om}}^{-1}) \quad (2)$$

Data analysis

The data were tested for normality (all models) and homogeneity of variances (GLM) using the Kolmogorov-Smirnov test and Levene's test, respectively, and if needed logarithmic (enchytraeid length and abundance, NH₄-N, soil moisture percentage), square-root (abundances of nematodes, collembolans and mites) and arcsin-transformations (proportion of bacterial-feeding nematodes) were used. The random effects of site *s* and block nested within location

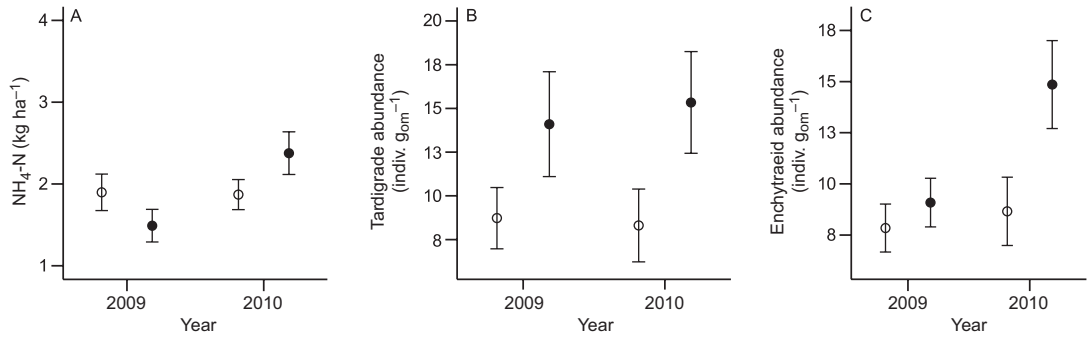


Fig. 1. (A) Main effects of sucrose amendment on $\text{NH}_4\text{-N}$ pool (mean \pm SE), and on the abundances of (B) tardigrades and (C) enchytraeids in the organic soil layer of two clear-cut Norway spruce forests. Filled circles denote sucrose addition (equalling 1 Mg C ha^{-1}) and open circles denote controls without sucrose. $N = 36$ (data pooled across the levels of wood ash and mounding treatments given non-significant interactions). Om = organic matter

$b(s)$, and the fixed effects of time t , sucrose C and the treatment combination k ($k = \text{control}, a, m, am$) were tested using the following mixed linear model:

$$y = \mu + s + b(s) + t + C + k + Ck + Ct + kt + Ckt + e \quad (3)$$

where a denotes wood ash and m mounding, and e is the error term. To account for the dependence between the repeated measurements, an unstructured, or — when the residual variances in 2009 and 2010 were equal — compound symmetrical covariance structure was used for the repeated effect of time. Because we were primarily interested in the effects of sucrose, factors that were not significant in the preliminary model (Eq. 3) were omitted from the final model. If a sucrose \times factor interaction was significant, the simple effects of sucrose at the levels of that factor were tested.

Variables measured once at the end of the study (plant biomass, pH and conductivity) were analysed using general linear models (GLM) obtained by omitting terms including t in Eq. 1. Statistical analyses were carried out with PASW 18.0.

Results

Sucrose increased the abundance of tardigrades (Fig 1 and Table 2) and in the second year also the abundance of enchytraeids (Fig. 1; $F_{1,137} = 14$, $p < 0.001$), but mites and collembolans were not

affected (data not shown). In 2010, Enchytraeid biomass was 16.3 kg ha^{-1} in the sucrose treatment, which is 94% more than in the control. Sucrose addition did not significantly affect the remaining mass of the cellulose strips (Table 2).

The size of the water-extractable $\text{NH}_4\text{-N}$ pool in the organic soil layer increased from 2009 to 2010 in the sucrose treatment ($F_{1,138} = 16$, $p < 0.001$), but remained the same in the control (Fig. 1; $F_{1,137} = 0.01$, $p = 0.906$). As compared with that in the control, sucrose addition tended to reduce the $\text{NH}_4\text{-N}$ pool in the first year ($F_{1,126} = 3.2$, $p = 0.076$), and increased it in the second year ($F_{1,134} = 4.4$, $p = 0.037$; Fig. 1).

Sucrose addition increased the abundance of nematodes without wood-ash fertilization ($F_{1,134} = 4.6$, $p = 0.033$; Table 2), but not in combination wood ash ($F_{1,134} = 2.2$, $p = 0.139$). The proportion of bacterial-feeding nematodes was $80\% \pm 2\%$ of total nematodes and the plant biomass was $250 \pm 50 \text{ kg ha}^{-1}$ irrespective of sucrose addition.

Sucrose addition increased soil moisture significantly (from $315\% \pm 9\%$ OM to $341\% \pm 9\%$ OM; Table 2). In Viitasaari and Ähtäri soil pH was 5.3 ± 0.04 and 6.0 ± 0.04 , and the conductivities were 3.02 ± 0.14 and $3.78 \pm 0.23 \text{ mS m}^{-1}$, respectively, regardless of sucrose addition.

Discussion

Key soil organisms

Because clear-cutting can increase the availability of inorganic N but can reduce the supply

of easily decomposable plant-derived carbohydrates, we expected that sucrose addition would increase the biomass of soil animals in the soil food web in clear-cut areas. Sucrose addition increased the abundances of tardigrades and enchytraeids partially supporting our hypothesis, but the abundances of mites and collembolans were not affected. Sucrose increases the body size, abundance, and population biomass of enchytraeids but the effects on nematodes are more variable (Nieminen 2008b, 2009a), and we are not aware of any previous studies on the effects of carbohydrate supply on tardigrades.

Sucrose addition did not reduce the proportion of bacterial-feeding nematodes as we hypothesized. This was unexpected given that Zygomycota fungi specialized at simple carbohydrates (Hanson *et al.* 2008) are also preferred food for hyphal-feeding nematodes (For example Nieminen and Setälä 2001). Glucose addition to the organic layer of forest soil also causes an accumulation of fungal triglycerols (Lundberg *et al.* 2001). A positive relation between the fungal:bacterial ^{13}C incorporation ratio and

the F:B ratio (Brant *et al.* 2006) suggests that the initial structure of the microbial community determines whether added C proceeds along the bacterial- or fungal-based food chain. Although the F:B ratio is related to the C:N ratio of the resource (Bossuyt *et al.* 2001), simple carbohydrates may be used by yeasts and bacteria in moist and nutrient-rich conditions (Bååth *et al.* 1978). Thus, it seems that organisms in the dominating bacterial-based food chain used part of the added sucrose in our clear-cut areas.

Carbohydrate addition to mineral soil frequently increases microbial biomass (e.g. Orwin *et al.* 2006). Glucose alone increased earthworm biomass in a beechwood, but simultaneous addition of inorganic nutrients was needed to increase microbial biomass (Scheu and Schaefer 1998). Similarly, glucose addition without simultaneous phosphorus (P) addition had few positive effects on soil animals other than earthworms in a mature beechwood (Maraun *et al.* 2001) suggesting that earthworms were superior competitors for new resources. The dominant enchytraeid species *Cognettia sphagnetorum*

Table 2. Full results of linear mixed models.

	Year	Sucrose	Ash	Mounding	Y × A	Y × M	Y × S	S × A	S × M
NH₄-N (kg ha⁻¹)									
Error df	137	133	133	133	137	137	137		
F	8.4	0.003	2.5	36.2	2.2	10.7	7.5		
p	0.004	0.052	0.118	< 0.001	0.136	0.001	0.007		
Enchytraeids (indiv. g_{om}⁻¹)									
Error df	142	135	135	135			142		
F	3.8	10.8	3	3.6			5.1		
p	0.052	0.001	0.084	0.06			0.025		
Moisture (%)									
Error df	143	135	135	135					
F	17.8	6.1	3.7	22.5					
p	< 0.001	0.015	0.057	< 0.001					
Nematodes (indiv. g_{om}⁻¹)									
Error df	143	134	134	134				134	
F	0.8	0.22	< 0.001	4.9				6.6	
p	0.385	0.64	0.994	0.029				0.011	
Tardigrades (indiv. g_{om}⁻¹)									
Error df	143	141							
F	0.001	4.3							
p	0.974	0.039							
Cellulose strip om^a									
Error df	65	65	n.a.	65					65
F	201	1.7	n.a.	24					2.7
p	< 0.001	0.2	n.a.	< 0.001					0.105

^a Remaining organic matter mass of cellulose strips.

may have prevented other soil animals from benefiting from resource addition also in our experiment. We cannot rule out direct consumption of sucrose by omnivorous enchytraeids. However, because the populations of nematodes and microbes are strongly correlated (Sánchez-Moreno *et al.* 2006), the increased abundance of microbial-feeding nematodes probably indicates enhanced microbial production. It remains unclear why in our study sucrose and wood ash increased nematode abundance when used separately, but not in combination.

Both sucrose addition and wood ash increased soil moisture more (25%) than can be explained by sucrose oxidation (about 2%). Thus, sucrose probably indirectly enhanced the water-holding capacity of soil. Gravimetric moisture content is positively correlated with microbial biomass and respiration (D'Angelo *et al.* 2005), and water-holding capacity is related to the soil organic carbon content. It is thus plausible that increased decomposer biomass enhanced the water-holding capacity of soils in our sucrose treatment. Sucrose addition increased soil moisture in a pot experiment (Nieminen 2009a), and combined sucrose and sawdust is known to increase soil moisture in field experiments (e.g. Szili-Kovács *et al.* 2007). Many different mechanisms (increased WHC, reduced evaporation) may be involved especially when woody material is applied as surface mulch. Also inorganic mulch such as gravel can increase soil moisture (Kraus 1998). As discussed by Nieminen *et al.* (2012), the hardly soluble wood ash probably acted as inorganic mulch in our study.

Cellulose decomposition

As we hypothesized, sucrose addition had no influence on the decomposition rate of cellulose strips in the clear-cut areas. In contrast, simple carbohydrates can reduce the decomposition rates of cellulose filters in microcosms (Orwin *et al.* 2006). However, the availability of inorganic N is much higher in the organic layer of disturbed forest soil (Nieminen 2010) than in the mineral soil used by Orwin *et al.* (2006). Because different microbial taxa are responsible for the decomposition of simple carbohydrates

and more complex C sources such as cellulose (Hanson *et al.* 2008), microbes utilizing added carbohydrates can compete for N with microbes decomposing native SOM. Consequently, the effect of labile C addition on the decomposition of more complex SOM depends on the availability of nitrogen. An addition of NH_4NO_3 to organic tundra soil removed the priming effect of glucose on SOM mineralization (Hartley *et al.* 2010). Similarly, the absence of a priming effect in our study suggests that the nitrogen availability was sufficient for both the bacteria utilizing added sucrose, and the decomposers of cellulose.

Nitrogen pools

Finally, we expected that sucrose addition would reduce the pool of water-extractable N because more N would be retained in the soil food web. The overall effect of sucrose was difficult to test, because the addition of sucrose altered the temporal dynamics of N. However, in support of our hypothesis sucrose addition tended to reduce the pool of water-soluble N in the organic soil layer in the first year. Consistent with this result, carbohydrate input reduces N availability in microcosms (Schmidt *et al.* 1997) and in forests (Stadler and Michalzik 1998). However, in our experiment the effect of sucrose was reversed in the second year. We do not know why the N pool increased in the second year after the clear cutting in the sucrose treatment. Possible reasons for this include the decomposition of N-containing compounds initially present in the soil, the release of N from newly formed microbial biomass, and increased enchytraeid activity.

At our study sites, the nematode community was strongly dominated by bacterial feeders (80%). As discussed above, sucrose was presumably utilized in the bacterial-based food chain. The dominance of the bacterial-based food chain may explain the relatively small reduction of N pools in our sucrose-amended soils. Organisms in bacterial-based food chains generally have higher turn-over rates and are considered to contribute more to net N mineralization than those in fungal-based ones (Osler and Sommerkorn 2007). For example, bacterial-feeding nematodes mineralize more N than fungal-feeding nema-

todes (Ferris *et al.* 1998, Chen and Ferris 2000). In addition, bacterial residues may decompose faster than fungal necromass (Strickland and Rousk 2010). The sucrose addition almost doubled enchytraeid biomass in our study. The N excretion rate of enchytraeids reported by Maraldo *et al.* (2011) applied to our sucrose treatment predicts an increase of ca. 1 kg N ha⁻¹ in the inorganic nitrogen pool, which is of the same magnitude as the increase in NH₄-N from 2009 to 2010. Enchytraeids may thus have contributed to the increase in N availability in the second year.

Nutrient immobilization in the soil food web is a potentially useful measure to prevent N loss from forest ecosystems which can also affect plant growth. Carbohydrate addition can reduce plant N content (Scheu and Schaefer 1998) and growth (Schmidt *et al.* 1997, Dunn *et al.* 2006), and alter the competition between different plant species (Nieminen 2009a). Incorporation of woody residues in forest soil has often been suggested as a means to reduce pools of inorganic N (O'Connell *et al.* 2004, Bulmer *et al.* 2007, Homyak *et al.* 2008, but see Busse *et al.* 2009), because C resources with highest cellulose concentration have the best net immobilizing capacity (Downs *et al.* 1996). According to our results, an addition of labile carbohydrates can reduce the N pool for a short time following clear cutting.

Conclusion

Although sucrose addition almost doubled the biomass of the keystone enchytraeid, *Cognettia sphagnetorum*, in the clear-cut areas, sucrose addition did not increase cellulose decomposition rate in our study. These results accord with a view that different organisms decomposed the added sucrose and cellulose. Our study supports a view that labile C addition aimed at reducing N loss from disturbed forest soil does not necessarily cause extra C loss from the recalcitrant soil organic matter. In our experiment, we used sucrose as the labile carbon source, because it has frequently been used as a means to enhance N immobilization in other experimental and real ecosystems. However, in our boreal forests the

addition of labile C reduced N pool only in the first year after clear-cutting. Thus, a single addition of simple carbohydrates cannot replace C resources with high cellulose contents.

Acknowledgements: The study was financially supported by Maj and Tor Nessling Foundation. We are pleased to express our appreciation to Mikko Räisänen for assisting with the field experiment, to UPM Kymmene Plc for permitting us to use the study areas, to FA Forest Ltd. for the wood ash, to Tea Sunden (Stora Enso Plc., Sunila Mill) for the cellulose strips, and to Anssi Lensu and Kari Nissinen for statistical advice.

References

- Aronsson K.A. & Ekelund N.G.A. 2004. Biological effects of wood ash application to forest and aquatic ecosystems. *J. Environ. Qual.* 33: 1595–1605.
- Bååth E., Frostegård Å., Pennanen T. & Fritze H. 1995. Microbial community structure and pH response in relation to soil organic matter quality in wood-ash fertilized, clear-cut or burned coniferous forest soils. *Soil Biol. Biochem.* 27: 229–240.
- Bååth E., Lohm U., Lundgren B., Rosswall T., Söderström B., Sohlenius B. & Wirén A. 1978. The effect of nitrogen and carbon supply on the development of soil organism populations and pine seedlings: a microcosm experiment. *Oikos* 31: 153–163.
- Bormann F.H., Likens G.E., Fisher D.W. & Pierce R.S. 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. *Science* 159: 882–884.
- Bossuyt H., Deneff K., Six J., Frey S.D., Merckx R. & Paustian K. 2001. Influence of microbial populations and residue quality on aggregate stability. *Appl. Soil Ecol.* 16: 195–208.
- Brant J.B., Sulzman E.W. & Myrold D.D. 2006. Microbial community utilization of added carbon substrates in response to long-term carbon input manipulation. *Soil Biol. Biochem.* 38: 2219–2232.
- Bulmer C., Venner K. & Prescott C. 2007. Forest soil rehabilitation with tillage and wood waste enhances seedling establishment but not height after 8 years. *Can. J. For. Res.* 37: 1894–1906.
- Busse M.D., Sanchez F.G., Ratcliff A.W., Butnor J.R., Carter E.A. & Powers R.F. 2009. Soil carbon sequestration and changes in fungal and bacterial biomass following incorporation of forest residues. *Soil Biol. Biochem.* 41: 220–227.
- Chatterjee A., Vance G.F., Pendall E. & Stahl P.D. 2008. Timber harvesting alters soil carbon mineralization and microbial community structure in coniferous forests. *Soil Biol. Biochem.* 40: 1901–1907.
- Chen J. & Ferris H. 2000. Growth and nitrogen mineralization of selected fungi and fungal-feeding nematodes on sand amended with organic matter. *Plant Soil* 218: 91–101.
- Dahlgren R.A. & Driscoll C.T. 1994. The effects of whole-

- tree clear-cutting on soil processes at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Plant Soil* 158: 239–262.
- D'Angelo E.M., Karathanasis A.D., Sparks E.J., Ritchey S.A. & Wehr-McChesney S.A. 2005. Soil carbon and microbial communities at mitigated and late successional bottomland forest wetlands. *Wetlands* 25: 162–175.
- Downs M.R., Nadelhoffer K.J., Melillo J.M. & Aber J.D. 1996. Immobilization of a ^{15}N -labeled nitrate addition by decomposing forest litter. *Oecologia* 105: 141–150.
- Dunn R.M., Mikola J., Bol R. & Bardgett R.D. 2006. Influence of microbial activity on plant-microbial competition for organic and inorganic nitrogen. *Plant Soil* 289: 321–334.
- Ekblad A. & Högborg P. 2000. Analysis of $\delta^{13}\text{C}$ of CO_2 distinguishes between microbial respiration of added C_4 -sucrose and other soil respiration in a C_3 -ecosystem. *Plant Soil* 219: 197–209.
- Feldkirchner D.C., Wang C., Gower S.T., Kruger E.L. & Ferris J. 2003. Effects of nutrient and paper mill biosolids amendments on the growth and nutrient status of hardwood forests. *For. Ecol. Manage.* 177: 95–116.
- Ferris H., Venette R.C., van der Meulen H.R. & Lau S.S. 1998. Nitrogen mineralization by bacterial-feeding nematodes: verification and measurement. *Plant Soil* 203: 159–171.
- Fontaine S., Barot S., Barré P., Bdioui N., Mary B. & Rumpel C. 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450: 277–280.
- Hannam K.D., Quideau S.A., Kishchuk B.E., Oh S.-W. & Wasylyshen R.E. 2005. Forest-floor chemical properties are altered by clear-cutting in boreal mixedwood forest stands dominated by trembling aspen and white spruce. *Can. J. For. Res.* 35: 2457–2468.
- Hanson C.A., Allison S.D., Bradford M.A., Wallenstein M.D. & Treseder K.K. 2008. Fungal taxa target different carbon sources in forest soil. *Ecosystems* 11: 1157–1167.
- Hartley I., Hopkins D.W., Sommerkorn M. & Wookey P.A. 2010. The response of organic matter mineralisation to nutrient and substrate additions in sub-arctic soils. *Soil Biol. Biochem.* 42: 92–100.
- Högborg M.N., Chen Y. & Högborg P. 2007. Gross nitrogen mineralization and fungi-to-bacteria ratios are negatively correlated in boreal forests. *Biol. Fertil. Soils* 44: 363–366.
- Homyak P.M., Yanai R.D., Burns D.A., Briggs R.D. & Germain R.H. 2008. Nitrogen immobilization by wood-chip application: protecting water quality in a northern hardwood forest. *For. Ecol. Manage.* 255: 2589–2601.
- Howard E.A., Gower S.T., Foley J.A. & Kucharik C.J. 2004. Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. *Global Change Biol.* 10: 1267–1284.
- Hyvönen R., Ågren G.I., Linder S., Persson T., Cotrufo M.F., Ekblad A., Freeman M., Grelle A., Janssens I.A., Jarvis P.G., Kellomäki S., Lindroth A., Loustau D., Lundmark T., Norby R.J., Oren R., Pilegaard K., Ryan M.G., Sigurdsson B.D., Strömberg M., van Oijen M. & Wallin G. 2007. The likely impact of elevated $[\text{CO}_2]$, nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytol.* 173: 463–480.
- Keenan R.J. & Kimmins J.P. 1993. The ecological effects of clear-cutting. *Environ. Rev.* 1: 121–144.
- Kraus H.T. 1998. Effects of mulch on soil moisture and growth of desert willow. *HortTechnology* 8: 588–590.
- Kurka A. 2001. The use of cellulose strips to study organic matter decomposition in boreal forested soils. *Boreal Environ. Res.* 6: 9–17.
- Kuzyakov Y., Friedel J.K. & Stahr K. 2000. Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* 32: 1485–1498.
- Lindo Z. & Visser S. 2003. Microbial biomass, nitrogen and phosphorus mineralization, and mesofauna in boreal conifer and deciduous forest floors following partial and clear-cut harvesting. *Can. J. For. Res.* 33: 1610–1620.
- Lundberg P., Ekblad A. & Nilsson M. 2001. ^{13}C NMR spectroscopy studies of forest soil microbial activity: glucose uptake and fatty acid biosynthesis. *Soil Biol. Biochem.* 33: 621–632.
- Maraldo K., Christensen B. & Holmstrup M. 2011. The excretion of ammonium by enchytraeids (*Cognettia sphagnetorum*). *Soil Biol. Biochem.* 43: 991–996.
- Maraun M., Alpehi J., Beste P., Bonkowski M., Buryr R., Migge S., Peter M., Schaefer M. & Scheu S. 2001. Indirect effects of carbon and nutrient amendments on the soil meso- and microfauna of a beechwood. *Biol. Fertil. Soils* 34: 222–229.
- Nieminen J.K. 2008a. Linking food webs to ecosystem processes: piecewise linear models of soil microcosms. *Ecol. Model.* 217: 87–94.
- Nieminen J.K. 2008b. Labile carbon alleviates wood ash effects on soil fauna. *Soil Biol. Biochem.* 40: 2908–2910.
- Nieminen J.K. 2009a. Combined effects of loose wood ash and carbon on inorganic N and P, key organisms and the growth of grasses and conifers in a pot experiment. *Plant Soil* 317: 155–165.
- Nieminen J.K. 2010. Labile carbon effects on nematodes, enchytraeids and N mineralization in Norway spruce forest soil. *Biol. Fertil. Soils* 46: 175–178.
- Nieminen J.K. & Setälä H. 2001. Bacteria and microbial-feeders modify the performance of a decomposer fungus. *Soil Biol. Biochem.* 33: 1703–1712.
- Nieminen J.K., Räisänen M. & Haimi J. 2012. Spot mounding and granulated wood ash increase inorganic N availability and alter key components of the soil food web in clear-cut Norway spruce forests. *For. Ecol. Manage.* 263: 24–30.
- O'Connor F.B. 1957. An ecological study of the enchytraeid worm population of a coniferous forest soil. *Oikos* 8: 161–199.
- Orwin K.H., Wardle D.A. & Greenfield L.G. 2006. Ecological consequences of carbon substrate identity and diversity in a laboratory study. *Ecology* 87: 580–593.
- Osler G.H.R. & Sommerkorn M. 2007. Toward a complete soil C and N cycle: incorporating the soil fauna. *Ecology* 88: 1611–1621.
- Pollierer M.M., Langel R., Körner C., Maraun M. & Scheu S. 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecol. Lett.*

- 10: 729–736.
- Rudolphi J. & Gustafsson L. 2005. Effects of forest-fuel harvesting on the amount of deadwood on clear-cuts. *Scand. J. For. Res.* 20: 235–242.
- Saarinen V.-M. 2006. The effects of slash and stump removal on productivity and quality of forest regeneration operations — preliminary results. *Biomass Bioenergy* 30: 349–356.
- Sánchez-Moreno S., Minoshima H., Ferris H. & Jackson L.E. 2006. Linking soil properties and nematode community composition: effects of soil management on soil food webs. *Nematology* 8: 703–715.
- Scheu S. & Schaefer M. 1998. Bottom-up control of the soil macrofauna community in a beechwood on limestone: manipulation of food resources. *Ecology* 79: 1573–1585.
- Schmidt M.G., Macdonald S.E. & Rothwell R.L. 1996. Impacts of harvesting and mechanical site preparation on soil chemical properties of mixed-wood boreal forest sites in Alberta. *Can. J. Soil Sci.* 76: 531–540.
- Schmidt I.K., Michelsen A. & Jonasson S. 1997. Effects of labile carbon on nutrient partitioning between an arctic graminoid and microbes. *Oecologia* 112: 557–565.
- Setälä H. 2000. Reciprocal interactions between Scots pine and soil food web structure in the presence and absence of ectomycorrhiza. *Oecologia* 125: 109–118.
- Siira-Pietikäinen A., Pietikäinen J., Fritze H. & Haimi J. 2001. Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. *Can. J. For. Res.* 31: 88–99.
- Smith V.H., Tilman G.D. & Nekola J.C. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environ. Pollut.* 100: 179–196.
- Smolander A., Kitunen V. & Mälkönen E. 2001. Dissolved soil organic nitrogen and carbon in a Norway spruce stand and an adjacent clear-cut. *Biol. Fertil. Soils* 33: 190–196.
- Sohlenius B. 1982. Short-term influence of clear-cutting on abundance of soil-microfauna (Nematoda, Rotatoria and Tardigrada) in a Swedish pine forest soil. *J. Appl. Ecol.* 19: 349–359.
- Stadler B. & Michalzik B. 1998. Linking aphid honeydew, throughfall, and forest floor solution chemistry of Norway spruce. *Ecol. Lett.* 1: 13–16.
- Strickland M.S. & Rousk J. 2010. Considering fungal:bacterial dominance in soils — methods, controls, and ecosystem implications. *Soil Biol. Biochem.* 42: 1385–1395.
- Yeates G.W., Bongers T., De Goede R.G.M., Freckman D.W. & Georgieva S.S. 1993. Feeding habits in soil nematode families and genera — an outline for soil ecologists. *J. Nematol.* 25: 315–331.
- Young M.J., Johnson J.E. & Thiel D.A. 1993. Effects of paper mill sludge and weed control on competing vegetation and growth of young red pine. *New Forests* 7: 345–361.