Soluble organic nitrogen in forests and adjacent clearcuts in British Columbia, Canada[1]

K.D. Hannam and C.E. Prescott

Abstract: Soluble organic N (SON) is recognized to be a source of N for plants, but the few studies of the effects of clear-cut harvesting on SON levels have reported inconsistent results. SON and soluble inorganic N (SIN) contents were measured in 1 mol/L KCl extracts of soil from forests and clearcuts in coastal cedar–hemlock forests near Port McNeill, B.C., and in high-elevation spruce–fir forests near Sicamous, B.C. To characterize the seedling root environment, sampling was confined to the top 20 cm of soil (consisting of forest floor at Port McNeill and forest floor plus mineral soil at Sicamous). Amino acid N and microbial N were determined on subsets of the samples. At both sites, SON content tended to be lower in clearcuts than in forests. Lower SON contents in clearcuts were caused by the removal of F-layer forest floor at Port McNeill and by reduced SON concentrations in the forest floor at Sicamous. Correlation analyses indicated close relationships between moisture content, SIN, SON, and microbial N. Changes in SON, SIN, and microbial N concentrations during buried bag incubations could not be explained simply by exchange among these three N pools. Free amino acid N accounted for 1–1.5% of the total SON content.

Résumé : L'azote (N) organique soluble est une source connue de N pour les plantes mais les quelques études qui portent sur les effets de la coupe à blanc sur les niveaux de N organique soluble rapportent des résultats inconsistants. Le contenu en N soluble organique et inorganique a été mesuré dans des extraits de sols au KCl (1 mol/L) provenant de forêts et de coupes à blanc dans des forêts côtières de thuya et de pruche près de Port McNeill et de forêts d'épinette et de sapin situées à haute altitude près de Sicamous, en Colombie-Britannique. Pour caractériser l'environnement du système racinaire des semis, l'échantillonnage a été limité aux premiers 20 cm de sol; ce qui correspond à la couverture morte à Port McNeill et à la couverture morte et au sol minéral à Sicamous. L'azote microbien et sous forme d'acides aminés a été mesuré sur des sous-ensembles des échantillons. Dans les deux stations, le contenu en N organique soluble avait tendance à être plus faible dans les coupes à blanc que dans les forêts. Le plus faible contenu en N organique soluble dans les coupes à blanc était dû à l'enlèvement de l'horizon F dans la couverture morte à Port McNeill et aux faibles concentrations de N organique soluble dans la couverture morte à Sicamous. Les analyses de corrélation indiquent qu'il y a une étroite relation entre le contenu en humidité, N inorganique soluble, N organique soluble et N microbien. Les changements dans la concentration de N organique soluble, de N inorganique soluble et de N microbien lors de tests d'incubation avec des sacs enfouis ne peuvent être expliqués simplement par les échanges entre ces trois pools de N. L'azote sous forme d'acides aminés représentait 1 à 1,5 % du contenu total de N organique soluble.

[Traduit par la Rédaction]

Introduction

Soluble organic N (SON) is the dissolved and potentially dissolved organic N (DON) that can pass through a 0.45-μm filter after being extracted in water or salt solution (Qualls 2000; Solinger et al. 2001). It is largely composed of complex humic materials (Kalbitz et al. 2000), whose chemical structure is extremely variable (Schulten and Schnitzer 1998). Until recently, SON was not measured in studies of soil N availability because organic N was considered to be unavailable for plant uptake (Kaye and Hart 1997; Chalot and Brun 1998; Lipson and Nasholm 2001). However, results from laboratory studies suggest that plants, often in association with mycorrhizae, are capable of obtaining N from amino acids and simple proteins (Stribley and Read 1980; Bajwa et al. 1985; Abuzinadah et al. 1986; Schobert and Komor 1987; Jones and Darrah 1994; Kielland 1994; Raab et al. 1999). Although free amino acids are typically a small fraction of SON (Qualls and Haines 1991; Qualls et al. 1991; Jones and Kielland 2002), results from field studies have indicated that plants can directly take up amino acids (Nasholm et al. 1998; Raab et al. 1999; Nordin et al. 2001).

Given that plants can access some organic N, SON uptake may be important in forest soils, where SON concentrations are frequently greater than soluble inorganic N (SIN) concentrations (Van Cleve and White 1980; Chang et al. 1995; Huang and Schoenau 1998; Devito et al. 1999). Increases in

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SIN concentration in forest soil have been reported for several years after timber harvesting (Vitousek and Melillo 1979; Edmonds and McColl 1989; Prescott 1997). Fewer studies have monitored changes in SON concentrations after timber harvesting and the results have been inconsistent. Smolander et al. (2001) found higher SON concentrations in humus from a clearcut than from an adjacent 60-year-old Norway spruce (*Picea abies* (L.) Karst.) stand in Finland for 5 years after harvesting. In Germany, differences in SON concentration between forest soil from 30-m gaps and adjacent uncut European beech (*Fagus sylvatica* L.) forest varied among sampling dates and soil layers (Bauhus 1998). On northern Vancouver Island, differences in SON concentration between uncut cedar–hemlock forests and 3- and 10-year-old clearcuts varied among forest floor layers (Chang et al. 1995).

In the present study, we first determine whether soil SON and SIN concentrations differ among uncut forests and adjacent clearcuts in two forest types in British Columbia. We then use (*i*) correlation analyses to explore for possible relationships between SON, SIN, microbial N, and moisture content and (*ii*) 1-month buried bag incubations to measure changes in SON concentration during incubation. Finally, we estimate the fraction of SON in these soils that can be attributed to free amino acids.

Materials and methods

Study sites

Three pairs of clearcuts adjacent to old-growth forests were selected at each of the two study sites. Both sites were already the subjects of research programs examining the effects of forestry activities on nutrient cycling and forest regeneration. At each site, the treatments were replicated three times for a total of six experimental units (i.e., three clearcuts and three old-growth forests).

Port McNeill

This site is near Port McNeill, B.C., in the very wet maritime subzone of the Coastal Western Hemlock (CWHvm) biogeoclimatic zone (Green and Klinka 1994). The forest is a mix of western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) with a dense shrub layer of salal (*Gaultheria shallon* Pursh) and *Vaccinium* spp. Topography is gently rolling; elevations are less than 300 m above sea level. Annual precipitation is 1700 mm, which falls predominantly as rain, and mean daily temperatures range from 3.0 °C in January to 13.7 °C in July (Prescott et al. 1993). Mineral soils are poorly drained Humo-Ferric Podzols of loamy texture overlying unconsolidated morainal and fluvial outwash material (Prescott et al. 1993). Forest floors are up to 1 m thick and are predominantly Humimors or Lignomors (Green et al. 1993).

Three blocks were selected at Port McNeill, each consisting of an uncut old-growth forest and an adjacent operationally harvested clearcut. Clearcuts in block 1 (50°36′N, 127°22′W) and block 2 (50°34′N, 127°17′W) were harvested in 1994–1995 and slash burned in 1996 and were 98.5 and 67.0 ha, respectively. The clearcut in block 1 was planted with a mix of western redcedar and western hemlock; the clearcut in block 2 was planted with western redcedar. The 32.1-ha clearcut in block 3 (50°39′N, 127°24′W) (located within a larger cutblock) was harvested in 1992–1993, slash burned in 1993, and planted with western redcedar in 1994.

Sicamous

This site is located near Sicamous, B.C. (50°49′N, 119°54′W), in the wet cold subzone of the Engelmann Spruce – Subalpine Fir (ESSFwc) biogeoclimatic zone (Lloyd et al. 1990). This high-elevation (1550–1750 m) forest has a mix of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) with a shrub layer of *Rhododendron albiflorum* (Hook.) and *Vaccinium* spp. The site has a north aspect and 20–40% slopes. Mean annual precipitation is 1300 mm (Parish et al. 1999), most of which falls as snow. Mean annual temperature is 1.2 °C, with a mean maximum in August of 11.5 °C and a mean minimum in December of –7.8 °C (D. Spittlehouse, British Columbia Ministry of Forests, Victoria, B.C., personal communication). The snow-free period is generally from late June to early October. On mesic sites, mineral soils are well to poorly drained Orthic Humo-Ferric Podzols of sandy loam texture overlying morainal deposits (Hope 1997). Forest floors are 4–5 cm thick and are predominantly Hemimors (Green et al. 1993).

Prior to this study, the area had been divided into three blocks based on elevation (Vyse 1999). Within each block, five treatments were applied: uncut forest, single-tree removal, and 0.1-, 1.0-, and 10-ha clearcuts. Only the three 30-ha uncut forests and three 10-ha clearcuts were used in this study. Clearcuts were harvested in the winter of 1994–1995 and were mounded but not burned prior to planting with Engelmann spruce in 1996.

Sample collection

In each forest and clearcut at both sites, a sampling area with similar plant species and a relatively homogeneous density of vegetation was selected. At Port McNeill, sampling areas were about 150 m × 150 m. At Sicamous, sampling areas were smaller than at Port McNeill (about 30 m × 30 m) to avoid disturbing other experiments. Within each sampling area, seven samples of mineral soil and (or) forest floor were collected from randomly selected sampling locations. Visibly disturbed soils and rotten wood were avoided; therefore, some randomly selected locations had to be rejected. At Port McNeill, samples were collected every 4 weeks between June and September 1999 and between May and September 2000. At Sicamous, samples were collected every 4 weeks from July to September in 1999 and 2000.

Sample collection was confined to the top 20 cm of forest soil to characterize the seedling root environment. In the uncut forest at Port McNeill, separate samples of F- and H-layer forest floor were collected. There was little or no F layer in the clearcuts at Port McNeill, so 20 cm of H-layer forest floor was collected. In both the clearcuts and uncut forest at Sicamous, the upper 20 cm of forest soil contained both mineral soil and forest floor because the forest floor was thin.

Prior to sample collection, the top layer of fresh litter was removed. Below this, samples were excavated intact using a trowel and root saw, placed in plastic bags, and stored in a

cooler with ice packs. In July 1999 and 2000, a second set of samples was collected from each of the three clearcuts and uncut forests at both sites for buried bag incubations (Eno 1960). These samples were collected adjacent to unincubated samples such that a pair of samples (one incubated and one unincubated) was collected from each sampling location. Samples for buried bag incubation were removed intact, using a trowel and root saw, placed in plastic bags (0.018 mm), and reburied in the hole from which they had been taken. These samples were incubated for about 4 weeks. After collection, all samples (incubated and unincubated) were kept cool, transported to the laboratory within 2 days of collection, and stored at 4 °C until extraction (a maximum of 5 days in 1999 and 3 days in 2000).

The bulk density of the top 20 cm of forest floor was determined at Port McNeill in July 2000 (Table 1). Within each sampling area, seven samples were excavated to a total depth of 20 cm using a 0.15 m × 0.15 m template (Little and Ohmann 1988). Thicknesses of F- and H-layer forest floors within the 20 cm depth of each sample were measured and each layer was placed in a separate bag for transport to the laboratory. Large roots and woody materials (greater than 5 mm in diameter) were removed, and each sample was weighed. Samples were dried for 24 h at 105 °C to determine moisture content. Bulk density was calculated by dividing the dry mass of the whole sample (kilograms) by the volume of the sample (cubic metres, i.e., 0.15 m × 0.15 m × thickness of the forest floor layer (metres)). Bulk densities of the top 20 cm of forest floor and mineral soil in forests and clearcuts at the Sicamous site were measured in July 2000 using the same technique.

Table 1. Characteristics of the soil horizons in the top 20 cm of forest soil at Port McNeill (forest floor only) and Sicamous (forest floor and mineral soil).

Treatment	Soil	Thickness (m)	Bulk density (kg/m^3)
Port McNeill			
Forest	F layer	0.03 (0.001)	70.0 (15.4)
	H layer	0.17 (0.001)	65.7 (9.5)
Clearcut	H layer	0.20 (0.00)	71.0 (7.9)
Sicamous			
Forest	Forest floor	0.06 (0.03)	87.4 (6.0)
	Mineral soil	0.14 (0.03)	674.3 (80.2)
Clearcut	Forest floor	0.05 (0.005)	103.0 (16.1)
	Mineral soil	0.15 (0.005)	676.7 (51.8)

Note: Each value is the mean of three blocks with standard deviation in parentheses.

SON and SIN

Immediately before extraction, each soil sample was sieved (4.7 mm) to homogenize the sample and to remove rocks, sticks, and pieces of roots. A 5- to 6-g (fresh mass) subsample was weighed and extracted in 50 mL of 1 mol/L KCl solution. On several occasions, a paired 5- to 6-g (fresh mass) subsample was weighed and extracted in distilled, deionized water. These additional extracts were used to compare the concentration of SON extracted in 1 mol/L KCl and in water. After shaking on ice for 1 h, soil solids were allowed to settle at 4 °C for 1 h and then the solution was gravity-filtered. The ice was used to prevent the solution from being heated by the antiquated shaker. In 1999, samples were gravity-filtered at room temperature through Whatman No. 42 or (equivalent) Fisher Q2 filter paper that had been preleached with 1 mol/L KCl solution. To minimize microbial activity and N mineralization during filtering, samples were gravity-filtered at 4 °C in 2000. However, differences in SIN concentration between 1999 and 2000 were not significant, suggesting that the temperature at which the samples were gravity-filtered did not strongly affect the results. A second portion of each soil sample was dried at 105 °C for 24 h to determine moisture content.

Extracts were stored at 4 °C until all samples had been extracted and gravity-filtered (2–5 days). Each extract was then vacuum-filtered through a 0.45-μm Durapore PVDF membrane filter. Some colloidal material will pass through a filter of this pore size along with the dissolved material (Rhea et al. 1996), but for simplicity the fraction passing through the filter was considered dissolved. A 5-mL aliquot was removed from the filtrate and placed in an acid-washed 40-mL glass vial for SON analysis. Nitrate and ammonium concentrations in the remaining filtrate were measured with a Lachat QuikChem AE autoanalyser (Lachat Instruments, Madison, Wis.) using the copperized cadmium reduction method and the salicylate–hypochlorite method (Mulvaney 1996), respectively.

A modified persulphate solution was used to convert dissolved N in the filtered soil extract to nitrate (Cabrera and Beare 1993). In 1999, 5 mL of persulphate solution was added to the 5 mL of soil extract in each glass vial. The volume of persulphate solution per vial was increased to 10 mL in 2000 to ensure complete oxidation of dissolved N. For each set of samples, the efficiency of total N recovery was confirmed by adding known concentrations of nitrate, ammonium, urea, or glycine to a bulk soil extract. There was no difference in the recovery of N from any of these standards in 1999 and 2000, which suggests that 5 mL of persulphate solution was sufficient to completely oxidize the N in the soil extracts. Vials were sealed with Teflon (PTFE)-lined caps, weighed, and autoclaved at 121 °C for 45 min. After autoclaving, each vial was reweighed to determine evaporation loss and then diluted with 5 mL of distilled, deionized water. Nitrate concentrations in the persulphate digests were measured using the same autoanalyser, and SON was calculated by subtracting the quantity of SIN (nitrate plus ammonium) in the extract from the quantity of total soluble N (as nitrate) in the extract. Cabrera and Beare (1993) suggested that KCl interferes with persulphate oxidation, but in a preliminary trial, there was no difference in recovery between standard solutions of ammonium, glycine, or urea in water and in 1 mol/L KCl.

Microbial N

To determine whether changes in SON were related to changes in the microbial N pool during incubation, microbial biomass N was measured using the chloroform fumigation–extraction method in concert with buried bag incubations in July 2000 (Horwath and Paul 1994). Net changes in microbial N were estimated by measuring microbial N in soil samples collected at the start of the incubation

period and in paired samples that were incubated in situ for 4 weeks. For each sample, approximately 10 g fresh mass of sieved soil was held under vacuum for 5 days after repeated evacuations with ethanol-free chloroform (Horwath and Paul 1994). Fumigated samples were extracted in 100 mL of 1 mol/L KCl and shaken on ice for 1 h. Extracts from fumigated samples were filtered and oxidized as described above for SON. Nitrogen released by chloroform fumigation–extraction was calculated by subtracting the total soluble N in unfumigated soil from the total soluble N in fumigated soil. A correction factor (K_{EN}) was not used in the biomass N calculation. Consequently, values reported here are a conservative estimate of the N contained in the microbial biomass and will be hereafter referred to as "microbial N".

Amino acid N

Water extracts for amino acid analysis were prepared from the forest floor and mineral soil samples collected in August 1999. Approximately 6 g fresh mass of sieved soil was extracted in 50 mL of distilled, deionized water and shaken on ice for 1 h. To avoid damaging the HPLC, samples were not extracted in 1 mol/L KCl solution (S. Silim, The University of British Columbia, personal communication). After shaking, samples were gravity-filtered at 4 °C through preleached Whatman No. 42 filter paper and then vacuum-filtered through a 0.45-μm PVDF membrane filter and placed in sterile vials. Extracts were stored frozen at –5 °C until January 2000.

A preliminary trial revealed that amino acid concentrations in the water extracts were too dilute for quantitative analysis using HPLC. To concentrate the extracts, they were thawed at room temperature and vigorously shaken. An 18-mL aliquot was removed from each sample and placed in a 20-mL glass scintillation vial. Aliquots were evaporated to dryness under vacuum at low temperature using a Savant Speed Vac (SC110A) equipped with a refrigerated vapor trap (RVT4104). Residues were dissolved in 1 mL of distilled, deionized water and the extracts were then filtered through 0.45-μm PVDF syringe filters.

Amino acids in the extracts were derivatized using AccQ.Fluor reagent (Waters Chromatography, Milford, Mass.). Amino acids were separated using a 3.9 m × 150 mm AccQ.Tag column (Waters Chromatography) on a Waters 600 LC system and detected with a Waters 474 scanning fluorescence detector using the gradient composition for analysis of unhydrolysed amino acid samples described by van Wandelen and Cohen (1997). An excitation wavelength of 250 nm was used and emission fluorescence was detected at 395 nm. The following amino acids were quantified: α-aminobutyric acid, γ-aminobutyric acid, alanine, arginine, asparagine, aspartic acid, cysteine, glutamic acid, glutamine, glycine, histidine, methionine, isoleucine, leucine, lysine, phenylalanine, proline, serine, threonine, tyrosine, and valine.

Statistical analysis

Most studies of soluble soil nutrients report concentrations by mass of soil, which can lead to misleading comparisons between forest floor and mineral soil. To avoid this problem, SON and SIN concentrations were calculated as a function of soil volume, which compensates for differences in soil bulk density.

Mean concentrations and contents of SON, SIN, and microbial N were calculated for each experimental unit on every sampling date. Overall means were then calculated as the average of all sampling dates for each experimental unit such that the overall $n = 3$. To examine treatment differences in SIN and SON content (kilograms per hectare) and concentration (grams per cubic metre), data were analysed using one-way ANOVA in a split (year) – split (month) randomized complete block design. At Port McNeill, where samples were collected three times in 1999 and five times in 2000, a split (date) randomized complete block design was used after determining that there were no interactions between treatment effects and year effects. Differences were considered significant if $p < 0.05$.

The percentage of KCl-extractable SON that could be extracted in water ($\%SON_{water}$) was calculated by site and soil type using the data from the paired samples extracted in water and KCl throughout the experiment. A $\%SON_{water}$ of 100% would indicate that 100% of the SON extractable in 1 mol/L KCl is also soluble in water. Thus, increasing values of $\%SON_{water}$ may indicate decreasing retention of SON by ion-exchange mechanisms because KCl solution removes materials bound to ion-exchange sites (Qualls 2000). Differences in $\%SON_{water}$ between forests and clearcuts were compared using two-tailed unpaired *t* tests and were considered significant if $p < 0.05$. In addition, the concentrations of SON in KCl extracts of samples on which amino acid analyses had also been performed were multiplied by the $\%SON_{water}$ values to estimate the water-extractable SON concentrations in these samples. These corrected SON concentrations were then used to determine the proportion of SON that can be attributed to amino acid N.

To examine the relationships between moisture content, SIN, SON, and microbial N, Pearson correlations were calculated by site and soil type across sampling dates and replicates. Nitrate data were log-transformed prior to analysis to meet the assumptions of normality and homogeneity of variance. Correlations were considered weak between 0.0 and 0.35, moderate between 0.35 and 0.65, and strong between 0.65 and 1.0. Correlations were considered statistically significant if $p < 0.05$.

Differences between forests and clearcuts in amino acid N content (grams per hectare) and concentration (grams per cubic metre) were analysed using one-way ANOVA in a randomized complete block design because amino acid N was measured on only one date at each site. Differences were considered significant if $p < 0.05$. All statistical analyses were performed using SAS version 6.12 (SAS Institute Inc., Cary, N.C.).

Results

SON contents (kilograms per hectare) were lower in the clearcuts than in the forests (Table 2); these differences were significant ($p = 0.030$) at Sicamous but not at Port McNeill. SIN contents were variable at both sites, and differences between forests and clearcuts were not significant.

The strength of differences between forests and clearcuts varied among forest floor and mineral soil layers (Table 2).

Table 2. Mean contents (kg/ha) and concentrations (g/m^3) of SON and SIN in the top 20 cm of forest soil at Port McNeill (forest floor only) and Sicamous (forest floor and mineral soil).

	Forest	Clearcut	*p*
Port McNeill			
Content			
SON	10.1 (3.0)	7.7 (1.5)	0.321
SIN	0.5 (0.1)	0.4 (0.04)	0.638
Concentration			
F layer			
SON	7.7 (1.1)		
SIN	0.4 (0.05)		
H layer			
SON	4.5 (0.9)	3.8 (0.4)	0.129
SIN	0.2 (0.04)	0.2 (0.02)	0.653
Sicamous			
Content			
SON	23.2 (1.7)*	17.5 (0.6)*	0.030
SIN	2.6 (2.2)	4.0 (2.2)	0.217
Concentration			
Forest floor			
SON	13.9 (1.6)*	6.9 (0.7)*	0.032
SIN	1.2 (0.5)	2.7 (1.0)	0.141
Mineral soil			
SON	10.9 (0.4)	9.3 (0.2)	0.274
SIN	1.3 (0.7)	1.8 (0.5)	0.473

Note: Each value is the mean of three blocks with standard deviation in parentheses. An asterisk indicates a significant difference at $p < 0.05$.

In the forest floor at Sicamous, SON concentrations (grams per cubic metre) were significantly greater in the forest than in the clearcuts ($p = 0.032$), but differences were not significant in the mineral soil. In H-layer forest floor at Port McNeill, the concentration of SON was similar in clearcuts and forests. There was no F-layer forest floor in the clearcuts, so differences between forests and clearcuts in the concentration of SON in the F layer could not be compared.

The ratio of SON content to SIN content was about 21 in the forests at Port McNeill and 9 in the forests at Sicamous. Although the ratio of SON to SIN was lower in the clearcuts (about 18 and 4 at Port McNeill and Sicamous, respectively), organic N remained the dominant form of soluble N.

Within the forests at Port McNeill, concentrations (grams per cubic metre) of SON ($p = 0.045$) and SIN ($p = 0.005$) were significantly greater in the F layer than in the H layer (Fig. 1). Within the forests at Sicamous, concentrations of SON and SIN were similar in the forest floor and mineral soil. The same was true in the clearcuts at Sicamous.

There was no difference between forests and clearcuts in $\%SON_{water}$ of H-layer forest floor at Port McNeill (Table 3). At Sicamous, there was a strong trend of greater $\%SON_{water}$ in forest floor ($p = 0.063$) and mineral soil from the clearcuts ($p = 0.051$), although differences were not statistically significant.

At both sites, there were significant positive correlations between moisture content and SON and between moisture content and microbial N (Table 4). There were also significant positive correlations between SON and microbial N in forest floor and mineral soil at Sicamous but not in forest floor at Port McNeill. There was no relationship between nitrate-N and moisture content, SON, or microbial N at either site, but both moisture content and SON correlated positively with ammonium-N at Port McNeill.

Fig. 1. Concentrations of SON and SIN in each soil layer sampled from clearcuts and forests at Port McNeill and Sicamous. Each value is the mean of three blocks. Error bars indicate 1 SD. Different letters indicate a significant difference between soil layers at $p < 0.05$.

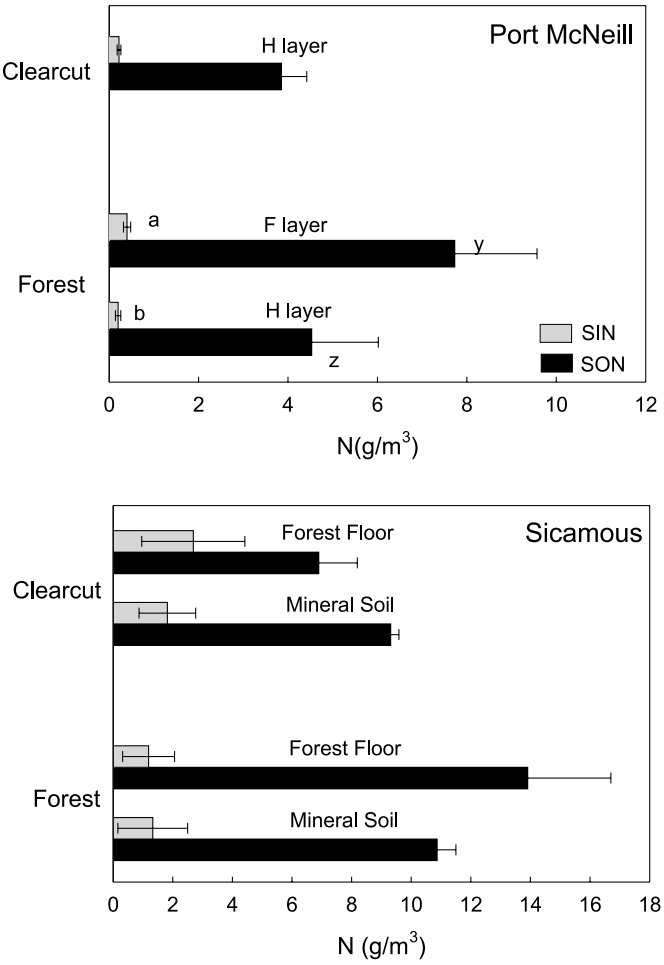


Table 3. SON extractable in water from the top 20 cm of forest floor (Port McNeill) or forest floor and mineral soil (Sicamous) expressed as a percentage ($\%SON_{water}$) of the SON extractable in 1 mol/L KCl from the same soils.

	Treatment		
Soil	Forest	Clearcut	*p*
Port McNeill			
F layer	31.3 (7.1)		
H layer	36.4 (3.2)	36.5 (7.4)	0.981
Sicamous			
Forest floor	19.9 (2.1)	31.5 (7.6)	0.063
Mineral soil	26.5 (2.3)	46.6 (12.4)	0.051

Note: Each value is the mean of three blocks with standard deviation in parentheses. The *p* values indicate the significance level of differences between forests and clearcuts compared using unpaired two-tailed *t* tests.

Table 4. Results of Pearson correlation analyses between moisture content (m^3 H_2O/m^3 soil) and SON, nitrate N, ammonium N, or microbial N concentration (g/m^3) and between SON concentration and nitrate N, ammonium N, or microbial N concentration across sampling dates and replicates in the top 20 cm of forest soil at Port McNeill (forest floor only) and Sicamous (forest floor and mineral soil).

		Port McNeill						Sicamous					
		F layer			H layer			Forest floor			Mineral soil		
		n	*r*	*p*	*n*	*r*	*p*	*n*	*r*	*p*	*n*	*r*	*p*
Moisture content	SON	166	0.323*	<0.001	333	0.384*	<0.001	252	0.366*	<0.001	252	0.445*	<0.001
	Nitrate N	185	0.045	0.562	428	0.029	0.730	252	0.022	0.730	252	–0.026	0.685
	Ammonium N	186	0.406	<0.001	428	0.211*	0.788	252	0.017	0.788	252	–0.039	0.537
	Microbial N	18	0.909*	<0.001	36	0.531*	0.020	36	0.386*	0.020	36	0.440*	0.007
SON	Nitrate N	167	–0.087	0.261	334	–0.009	0.109	252	–0.101	0.109	252	–0.107	0.784
	Ammonium N	167	0.455*	<0.001	334	0.209*	0.761	252	0.019	0.761	252	0.047	0.456
	Microbial N	18	–0.097	0.702	36	0.303	<0.001	36	0.464*	<0.001	36	0.638*	0.004

Note: Note that a correction factor (K_{EN}) was not used to estimate microbial N. An asterisk indicates a significant relationship at $p < 0.05$.

SON and SIN concentrations (grams per cubic metre) in forest floor (Port McNeill and Sicamous) and mineral soil (Sicamous) showed similar changes after 1 month of incubation in July 1999 (Fig. 2). The concentration of SON declined at both sites, while that of SIN changed little at Port McNeill and increased at Sicamous. The decline in SON during incubation could not be directly attributed to mineralization because the change in SON was greater than the change in SIN at Port McNeill and was less than the change in SIN in the clearcuts at Sicamous.

A second 1-month incubation in July 2000 was used to determine if the decline in SON observed after the July 1999 incubation could be explained by microbial uptake. However, the concentration of SON increased during the second incubation (Fig. 3). The only exception was the mineral soil from the forests at Sicamous in which the concentration of SON declined. Contrary to expectations, mean microbial N concentrations also increased during the second incubation in all soil layers at both sites.

SON and amino acid N were extracted differently, so the pools cannot be directly compared. However, using concentrations of water-extractable SON estimated with the $\%SON_{water}$ values, and assuming that the composition of SON is similar in water and 1 mol/L KCl extracts, this indicates that about 1–1.5% of the SON extracted from these soils is in the form of free amino acids. Although amino acid N appears to be a very small fraction of the SON in these soils, its distribution was similar to that of SON. Mean amino acid N contents (grams per hectare) were higher in forests than in clearcuts (Table 5), but differences were not significant.

Alanine and threonine were among the five most abundant amino acids in every mineral soil and forest floor layer sampled (Table 6). High concentrations of proline, serine, glycine, and glutamine were often found. At Port McNeill, arginine was abundant in the F layer but not in the H layer of either forests or clearcuts. At Sicamous, arginine was abundant in mineral soil from the forests.

Discussion

At both sites, SON contents tended to be higher in the forests than in the clearcuts, although differences were not statistically significant at Port McNeill. The cause of lower SON contents in the clearcuts differed between the two sites. In the forests at Port McNeill, the top 20 cm of forest floor included both an F and an H layer. Only H-layer forest floor was present in the clearcuts at Port McNeill because the F layer had been displaced, burned, or degraded. The similar SON concentrations in H-layer forest floor from the clearcuts and forests agree with an earlier study in the same forest type in which similar SON concentrations were found in H-layer forest floor from old-growth forest and 3- and 10-year-old clearcuts (Chang et al. 1995). Therefore, the trend toward higher SON contents in the forests at Port McNeill can be attributed to the SON-rich F layer, which was only present in the forests.

At Sicamous, differences in SON content between forests and clearcuts were due to lower SON concentrations in the forest floor of the clearcuts. Such a strong reduction in the concentration of SON in forest floor from clearcuts has not

Fig. 2. Net change in the concentrations of SON and SIN at Port McNeill (forest floor only) and Sicamous (forest floor and mineral soil) during 1-month buried bag incubations in July 1999. Each value is the mean of three blocks. Error bars indicate 1 SD.

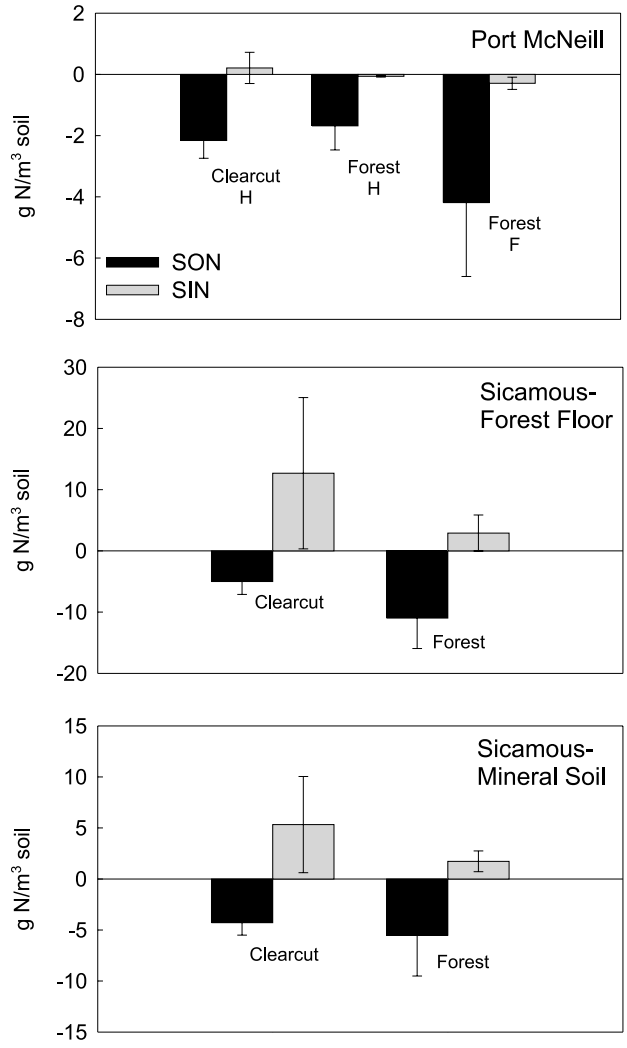
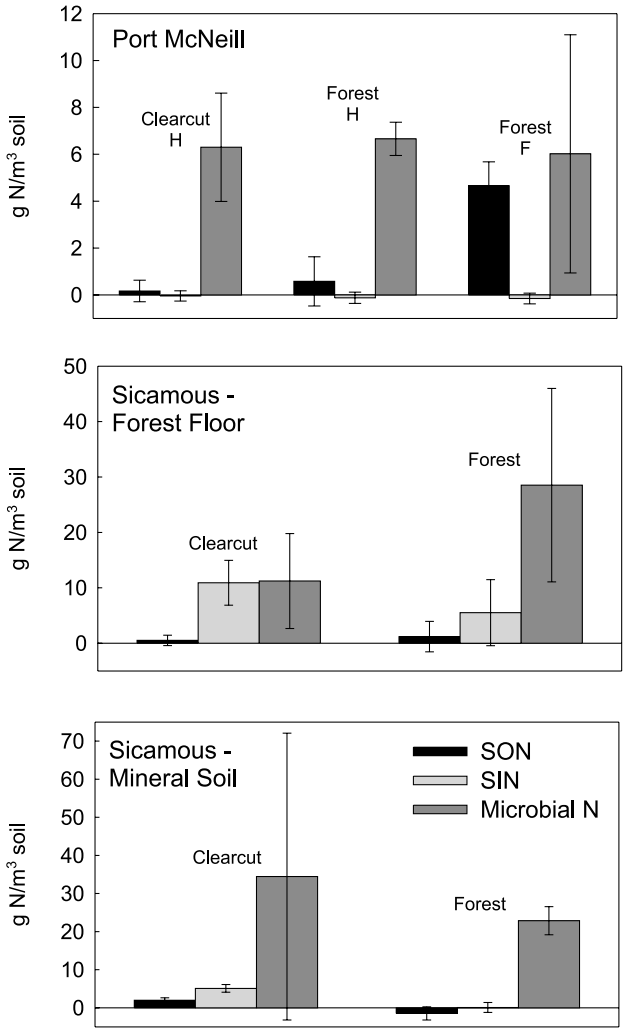


Fig. 3. Net change in the concentrations of SON, SIN, and microbial N at Port McNeill (forest floor only) and Sicamous (forest floor and mineral soil) during a 1-month buried bag incubation in July 2000. Note that a correction factor (K_{EN}) was not used to estimate microbial N. Each value is the mean of three blocks. Error bars indicate 1 SD.



been documented elsewhere. Bauhus (1998) found higher concentrations of SON in O_H-layer forest floor from harvested gaps than from the surrounding beech forest. Higher SON concentrations were also reported in humus from a clearcut than in humus from an adjacent Norway spruce forest up to 5 years after logging (Smolander et al. 2001). Greater concentrations of SON may occur during the first few years after timber harvesting because logging slash is rich in DON (Emmett et al. 1991; Qualls et al. 2000), but it is not clear how long logging slash remains a DON source. Scarlet oak (*Quercus coccinea* Muenchh.), red maple (*Acer rubrum* L.), and black locust (*Robinia pseudoacacia* L.) logs were rich sources of dissolved organic C for 7 years after cutting, but the N content of solution leached from these logs was not determined (Mattson et al. 1987).

There are several possible mechanisms for the reduction of SON concentration in the forest floor following timber harvesting at Sicamous. Aboveground litter and fine roots are important sources of SON (e.g., Qualls and Haines 1992; Huang and Schoenau 1998; Chapman et al. 2001); therefore,

Table 5. Content of amino acid N in the top 20 cm of soil in forests and clearcuts at Port McNeill and Sicamous.

Treatment	Amino acid N (g/ha)
Port McNeill	
Forest	31.1 (13.6)
Clearcut	15.9 (12.0)
Sicamous	
Forest	123.7 (83.5)
Clearcut	47.3 (25.1)

Note: Each value is the mean of three blocks with standard deviation in parentheses. Differences in amino acid N contents between forests and clearcuts at each site were not significantly different at $p < 0.05$.

Table 6. Total amino acid N concentrations (mg/m^3) and concentrations of the most common amino acids in the top 20 cm of soil in forests and clearcuts at Port McNeill and Sicamous.

	Port McNeill			Sicamous			
	Forest		Clearcut	Forest		Clearcut	
Amino acid	F layer	H layer	H layer	Forest floor	Mineral soil	Forest floor	Mineral soil
Alanine	3.0 (1.0)	1.0 (0.8)	0.6 (0.4)	1.3 (0.9)	10.0 (8.6)	2.5 (3.6)	2.4 (1.7)
Arginine	5.6 (4.8)	0.3 (0.6)	0.4 (0.7)	2.0 (1.9)	7.3 (12.0)	3.0 (2.6)	1.5 (2.7)
Glutamine	2.4 (1.5)	0.6 (0.2)	0.4 (0.1)	2.1 (1.1)	4.4 (1.8)	2.8 (3.5)	1.1 (0.4)
Glycine	1.9 (0.8)	1.6 (1.1)	0.6 (0.3)	0.9 (0.2)	8.9 (8.9)	1.6 (1.6)	2.7 (2.3)
Proline	4.0 (1.4)	0.6 (0.1)	2.9 (3.3)	2.1 (1.1)	17.5 (16.1)	3.9 (4.8)	4.8 (1.4)
Serine	1.3 (0.5)	2.1 (1.6)	0.6 (0.2)	0.6 (0.2)	5.7 (5.7)	0.9 (0.9)	3.0 (3.0)
Threonine	4.9 (1.4)	0.9 (0.4)	0.6 (0.4)	1.0 (0.4)	5.2 (4.3)	3.3 (2.7)	1.8 (1.2)
Total	36.6 (12.2)	11.4 (6.6)	7.9 (6.0)	15.1 (5.0)	93.4 (73.8)	28.7 (34.1)	22.8 (11.2)

Note: Each value is the mean of three blocks with standard deviation in parentheses. Differences between forests and clearcuts or between forest soil layers within forests or clearcuts were not significant.

removal of trees by timber harvesting can be expected to reduce SON concentrations. However, SON concentrations are not controlled solely by plant inputs because SON can increase or decrease during incubations (Hart et al. 1994; Huang and Schoenau 1998; Devito et al. 1999; Schmidt et al. 1999), when litter and throughfall (as well as leaching losses and plant uptake) are excluded.

Reductions in the ability of forest soil to abiotically retain SON could also lower the concentration of SON in the clearcuts. Differences between forests and clearcuts in the extractability of SON from forest floor and mineral soil in water and in salt solution suggest decreased retention of organic N by ion exchange in soil from clearcuts at Sicamous. Reduced sorption of SON in the clearcuts at Sicamous may be exacerbated by increased water flow. Hagedorn et al. (2000) found that sorption of organic material onto mineral soil particles decreased under higher water flow velocities, resulting in greater losses of DON in soil leachate. In the first year following harvesting, soil leachate volumes were greater in a clearcut than in a forest at Sicamous, and the annual flux of DON in leachate from the clearcut was more than double that from the adjacent forest (Feller 1997). Thus, reduced abiotic retention of SON may be one reason for reduced concentrations of SON in the forest floors of clearcuts at Sicamous.

Soil moisture contents, SON concentrations, and microbial N concentrations were related to one another, but it is not clear what processes drive these relationships. In the F layer and H layer at Port McNeill, there was a positive correlation between moisture content and SON and between moisture content and microbial N. In forest floor and mineral soil at Sicamous, there was a positive correlation between moisture content and SON, between moisture content and microbial N, and between SON and microbial N. The positive relationship between SON and microbial N contrasts with previous findings that suggested a source–sink relationship between SON and microbial N (Hart and Firestone 1991; Hart et al. 1994). Instead, our findings apparently support the hypothesis that SON production is higher in wet soils because of a larger microbial population (Van Cleve and White 1980; Williams 1992). However, this could also be the result of high SON uptake by the microbial biomass coupled with high SON production.

The results of the buried bag incubations indicated that changes in forest soil SON, SIN, and microbial N concentrations could not be explained simply by exchange among these three pools. This indicates that (*i*) the concentration of SON can increase or decrease during incubation and (*ii*) changes in forest soil SON concentrations cannot be directly explained by losses to or gains from the microbial N or SIN pools.

Amino acid N accounted for only 1–1.5% of the SON in the mineral soil and (or) forest floor at both sites. This is much lower than values reported for taiga forest soil, where Jones and Kielland (2002) estimated that amino acids were 4–20% of the total SON. Kielland (1995) suggested that protease activity is enhanced under conditions of low soil pH, resulting in a SON pool that is relatively rich in free amino acids. However, the pH of forest soils at Port McNeill and Sicamous can be lower than 3.7, which is the lowest pH value reported for soils at Kielland's (1994) study sites. Therefore, depressed protease activity is probably not the reason for lower concentrations of amino acid N in forest soil at Sicamous and Port McNeill compared with taiga forest soil.

The most abundant amino acids (alanine, threonine, arginine, proline, serine, glycine, and glutamine) are, with the exception of proline, those reported to be most abundant at other sites (Ivarson and Sowden 1966; Kielland 1995; Turnbull et al. 1995; Schmidt and Stewart 1997; Nordin et al. 2001). All of the dominant amino acids except arginine are neutral amino acids. Neutral amino acids probably dominate soil extracts because they diffuse readily in soil solution (Jones and Darrah 1994; Kielland 1994).

Arginine was the only amino acid that showed differences between soil layers or between forests and clearcuts, being highest in F-layer forest floor at Port McNeill and in mineral soil from the forests at Sicamous. Elevated levels of arginine could result from contamination of soil samples by damaged fine roots because N is stored as arginine in plant roots (Van den Driessche and Webber 1977; Lipson et al. 1996). However, other studies in which concentrations of amino acids in soil extracts and plant roots were compared found no evidence for contamination of soil samples by amino acids from root tissue (Ivarson and Sowden 1969; Kielland 1995).

In summary, SON contents tended to be lower in the clearcuts than in the forests at both sites. This was attributed to the removal of the SON-rich F layer at Port McNeill and to the reduction in forest floor SON concentration at Sicamous. The reduced SON concentrations in forest floor

from the clearcuts at Sicamous may be due, at least partly, to reduced abiotic retention of SON. The ratio of SON to SIN was about 21 and 18 in the forests and clearcuts, respectively, at Port McNeill and about 9 and 4 in the forests and clearcuts, respectively, at Sicamous. Soil moisture contents, SON concentrations, and microbial N concentrations were related, but it is not clear what processes drive these relationships. Changes in SON, SIN, and microbial N concentrations during buried bag incubations could not be explained simply by exchange among these three pools. Like SON, amino acid N contents tended to be higher in the forests than in the clearcuts at both sites, although amino acid N was only a small fraction of the SON. Arginine was the only amino acid whose abundance tended to differ between soil layers or between forests and clearcuts, and this pattern did not appear to be related to inputs of arginine from damaged fine roots. Future studies are required to examine gross changes in these N pools, to more precisely describe the SON pool, and to measure abiotic sorption of SON in these soils.

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