DOES CLEARCUTTING AFFECT THE QUANTITY OF SOLUBLE ORGANIC NITROGEN IN FOREST SOIL?

by

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ABSTRACT

Soluble organic N (SON) is often more abundant than soluble inorganic N (SIN) in forest soils. The effects of forest management on the abundance of SON in forest soils are of interest because plants can take up some of this N. Studies investigating the impact of logging on SON concentrations have found inconsistent results. Concentrations of SON and SIN were measured in forests and clearcuts in coastal cedar-hemlock forests near Port McNeill, B.C. and in high-elevation spruce-fir forests near Sicamous, B.C. Soil samples were collected to a cumulative depth of 20 cm in order to characterize the forest soil environment exploited by young seedlings. At Port McNeill, samples from the forest consisted of F- and H-layer forest floor. In the clearcuts, samples consisted of H-layer forest floor only, because the F layer was absent. At Sicamous, samples of forest floor and mineral soil were collected from both the forest and clearcuts. SON was determined in 1 M KCl extracts using persulphate oxidation. Amino acid-N and microbial N were determined on separate subsets of the samples. At both sites, forest soil SON content was significantly greater than SIN content. Free amino acid-N was estimated to comprise 1 to 1.5 % of the total SON content. SON content tended to be higher in the forests than in the clearcuts at both sites but differences were significant at Sicamous only. At Port McNeill, SON content tended to be higher in the forests than in the clearcuts because of the presence of a SON-rich F layer, which was absent in the clearcuts. At Sicamous, SON content tended to be higher in the forests than in the clearcuts because forest floor SON concentrations were significantly lower in the clearcuts. Correlation analysis indicated close relationships between moisture content, SIN, SON and microbial N. However, buried bag incubations suggested that changes in forest soil SON, SIN and microbial N concentrations cannot be explained simply by exchange among these three N pools.

Key Words: cedar-hemlock, clearcut, forest floor, free amino acids, microbial N, soluble inorganic N (SIN), soluble organic N (SON), spruce-fir

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INTRODUCTION

RATIONALE

The temperate coniferous forests of North America are widely considered to be nitrogen-limited (Fisher and Binkley 2000). As a result, the impact of timber harvesting on N availability has been the subject of intense study. Research has focussed primarily on the availability of nitrate and ammonium because plants were originally believed capable of taking up only inorganic N-forms. The findings a) that soluble organic N (SON) is often more abundant than soluble inorganic N (SIN) in forest soil (e.g. Van Cleve and White 1980; Huang and Schoenau 1998; Devito et al. 1999), and b) that plants can access organic N (e.g. Bajwa and Read 1985; Finlay et al. 1992; Nasholm et al. 1998), made it clear that the effects of timber harvesting on the availability of SON required further study.

Clearcutting is one of the most common and controversial forestry practices (Keenan and Kimmins 1993). Clearcutting can reduce a forest's total N capital by removing the N stored in live tree stems and foliage (Keenan and Kimmins 1993; Ballard 2000; Fisher and Binkley 2000). In addition, inorganic N concentrations are often elevated in forest soil for several years after harvest (e.g., Vitousek and Melillo 1979; Edmonds and McColl 1989; Prescott 1997). This flush of inorganic N can lead to increased losses of N via leaching, volatilization and de-nitrification (Vitousek and Melillo 1979; Feller and Kimmins 1984).

Although post-harvest changes in SIN have been the subject of numerous studies, few have examined the impact of timber harvesting on the abundance of SON in forest soil. Changes in the quantity and quality of SON following clearcutting may have implications for long-term site

productivity and nutrient availability. This research compares the quantity of SON and amino acid-N in clearcuts and uncut forests in two forest types in British Columbia.

LITERATURE REVIEW

What is SON?

SON is the dissolved and potentially dissolved organic N that can pass a 0.45 μm filter after being extracted in water or salt solution (Qualls 2000; Solinger et al. 2001). In some studies, the terms SON and DON (dissolved organic N) are used synonymously. However, this is misleading, because DON refers to the organic N already in solution (Murphy et al. 2000; Qualls 2000). More appropriate synonyms for SON are 'extractable organic N' (Chang et al. 1995; Bauhus 1998) or 'extractable DON' (Perakis and Hedin 2001; Smolander et al. 2001). In this paper, 'SON' will be used to describe organic N extracted from soil or humus, and 'DON' will be used to describe organic N collected in stream water, soil leachate or soil solution.

A number of studies have measured the quantities of SON and SIN in non-agricultural soils (Table 1). Values of SON reported in different studies must be compared with caution because of the range of soil types sampled and the variety of extractants used. The quantity of SON extracted from soil depends on both the nature and the strength of the extractant (Bauhus 1998; Shepard et al. 2001). Concentrations of SON in the forest floor and mineral soil range from 0 to 1000 μg/g. There are no obvious differences in the concentrations of SON between coniferous and deciduous forests, nor is there a clear relationship between SON concentration and the type of extractant used. In all but one study (Smolander et al. 2001), the concentration of SON was at least twice that of SIN.

Table 1. Summary of soluble organic N (SON) measurements (including values estimated from graphs or derived from information given in the article) in non-agricultural soils.

Ecosystem	Extractant	Soil type	Concentration of SON	SON:SIN	Authors
60-year-old paper birch forest in Alaska	2 M KCl	Forest floor	200-1000 μg/g	2-6	Van Cleve and White (1980)
Sitka spruce & Scots pine plantations in Scotland	1M KCl	Forest floor	0-18 kg/ha	0-6	Williams (1992)
		Mineral soil	0-45 kg/ha	0-7.5	
Coastal western redcedar/western hemlock forest in British Columbia	0.5 M K_2SO_4	F-layer forest floor	40-140 μg/g	-	Chang et al. (1995)
		H-layer forest floor	30-120 μg/g	-	
Sparsely vegetated slope in Nevada	Water	0-8 cm mineral soil	6.5 μg/g	~20	Rhea et al. (1996)
		8-16 cm mineral soil	5.1 μg/g	~170	
Heath tundra	2 M KCl	Entire 3 cm organic layer	-	9-25	Kielland (1997)
Tussock tundra		Top 10 cm of organic layer		30	
Boreal aspen stand in Saskatchewan	Water	Oi-layer forest floor	28-334 μg/g	3-9	Huang and Schoenau (1998)
		Oe-layer forest floor	2-199 μg/g	3-6	
		Oa-layer forest floor	2-306 μg/g	4-19	
		E-horizon	0-97 μg/g	5-16	

Table 1. (continued)

Ecosystem	Extractant	Soil type	Concentration of SON	SON:SIN	Authors
European beech forest in Germany	0.5 M K_2SO_4	O_F-layer forest floor	48-57 μg/g	-	Bauhus (1998)
		O_H-layer forest floor	35-39 μg/g	-	
		0-5 cm mineral soil	17-27 μg/g	-	
		5-10 cm mineral soil	11-22 μg/g	-	
		10-20 cm mineral soil	15-28 μg/g	-	
Mixed deciduous & coniferous forest in Ontario	2 M K_2SO_4	Top 10 cm of LFH & A-horizon	25-100 μg/g	5-20	Devito et al. (1999)
Peatland in Ontario		Top 10 cm of peat	150-300 μg/g	3-6	
60-year-old Norway spruce forest in Finland	Water	Humus layer	31 μg/g	0.78	Smolander et al. (2001)

The size of a nutrient pool does not reflect how rapidly it is cycled (Davidson et al. 1992). Thus, SON could be more abundant than SIN because a) more SON is released into the soil than SIN or b) slow rates of decomposition and/or immobilization cause more SON to accumulate than SIN. Although some studies have considered SON to be a pool of easily mineralisable N (e.g. Smith et al. 1980; Fahey et al. 1985; Beauchamp et al. 1986), the decomposition of organic N in leachate from litter, forest floor and mineral soil in Appalachian deciduous forest was actually very slow (Qualls and Haines 1992). Using ^{15}N-isotope dilution techniques in forest floor from

an Alaskan paper birch ecosystem, Van Cleve and White (1980) estimated a turnover time of less than 3 days for the 'rapidly equilibrating' nitrate and ammonium pools, and a turnover time of 54 to 94 days for the SON pool. This suggests that SON accumulates in the soil because it turns over more slowly than SIN.

The slow turnover of SON is probably a function of its complex organic structure. It is not possible to characterize the specific compounds comprising SON because it is largely composed of complex humic materials (Kalbitz et al. 2000), which are extremely variable (Schnitzer and Khan 1978; Schulten and Schnitzer 1998). However, fractionation on the basis of molecular surface properties has been used to characterize and quantify the types of organic molecules in which SON and DON are bound (Qualls and Haines 1991). Using these methods, it has been shown that SON and DON are dominated by hydrophobic and hydrophilic acids, which are large polyphenolics with varying concentrations of carboxyl groups (e.g. Qualls and Haines 1991; Northup et al. 1995; Smolander et al. 2001). Labile sugars, proteins and amino acids are only a small fraction of DON (Qualls and Haines 1991; Qualls et al. 1991), although their abundance can increase during early snowmelt (Yavitt and Fahey 1984) or after re-wetting of dry soil by autumn rains (Abuarghub and Read 1988b).

Why is SON important?

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, plants appear to have a number of mechanisms for obtaining N from organic sources. In the laboratory, it has been shown that tree seedlings, in association with some ericoid and ectomycorrhizal fungi, can access N from organic sources such as amino acids and simple proteins (e.g., Stribley and Read 1980; Bajwa and Read 1985;

Finlay et al. 1992). Some species of arctic and alpine plants (*i.e.*, mosses, lichens and sedges) can access organic N without the aid of mycorrhizal symbionts or with only weak mycorrhizal associations (Schimel and Chapin 1996; Kielland 1997; Raab et al. 1999).

The ability to access organic N may be a competitive advantage in N-limited forests (Northup et al. 1995; Northup et al. 1998; Raab et al. 1999). Thus far, however, there is no evidence that plants deplete the soluble organic N pool. Leachate from incubated soil cores covered with living moss and grasses had higher concentrations of DON than soil cores without vegetation (Chapman et al. 2001). In a field study in North Wales, lysimeters placed in forest soil below *Picea sitchensis* seedlings or *Agrostis capillaris* plants collected similar or slightly higher amounts of DON than those under bare soil (Emmett et al. 1991).

Plants as a source of SON

Organic N can be released from the overhead canopy as throughfall or in leaf litter leachate (Figure 1). In a deciduous forest in the Appalachians, concentrations of DON from throughfall were highest in the spring and summer (Qualls and Haines 1991; Qualls and Haines 1992). Throughfall may play an even greater role in coniferous forests, given that Currie et al. (1996) found that DON concentrations in throughfall were the same or higher in a red pine stand than in a hardwood stand in Massachusetts. The concentrations of DON and SON rise sharply in some deciduous forest floors in autumn (Qualls et al. 1991; Huang and Schoenau 1998), but leaf litter is probably an important source of SON year-round, with the majority being leached from litter at a slow and sustained rate (Qualls et al. 1991). Nitrogen in leachate collected over 15 weeks from the litter of a variety of deciduous and coniferous tree species was shown to be 93-100% in an organic form (Magill and Aber 2000).

Indirect evidence suggests that root tissue is also an important SON source. In both coniferous and deciduous forests, the production of fine roots can be at least twice that of aboveground litter (Fogel and Hunt 1983; Fahey and Hughes 1994). In addition, nutrient re-translocation prior to fine root senescence is believed to be low (Nambiar 1987; Aerts et al. 1992), which means that decaying roots are probably an organic N-rich substrate. Aerts et al. (1992) estimated organic N inputs of 1.8 $g/m^2/yr$ from *Calluna* roots and between 1.3 and 19.7 $g/m^2/yr$ from roots of grass species. Declining concentrations of DON in leachate from soil cores were observed two weeks after the removal of vegetation (Chapman et al. 2001). This slow decline in DON was attributed to the degradation of residual fine root tissue remaining in the soil. Clearly, living plants are an important source of SON.

What happens to SON after timber harvesting?

Because clearcutting results in the removal of the overhead canopy and a reduction in the density of fine roots in the forest soil (Parsons et al. 1994b; Hagerman et al. 1999), SON and DON levels could be expected to decline following timber harvesting. Indeed, Parsons et al. (1994a) found that the concentration of DON in soil solution from a Wyoming lodgepole pine forest declined with increasing basal area removal. However, reductions in the concentrations of SON and DON following logging are not consistent. The concentration of DON increased after clearcutting a Douglas-fir forest in Oregon (Sollins and McCorison 1981) and a deciduous forest in the Appalachians (Qualls et al. 2000). The concentration of SON was also higher in humus from a clearcut than an adjacent Norway spruce forest in Finland (Smolander et al. 2001).

It is doubtful that SON accumulates after logging as a result of decreased plant uptake because most of this N is bound in complex humic structures, which are probably not available for direct uptake by plants. Instead, an increase in SON and DON in the first few years following timber

harvesting may be due to increased leaching inputs of soluble organics from logging slash (Emmett et al. 1991; Qualls et al. 2000). One year after harvesting a Sitka spruce stand in Wales, the forest floor in a conventionally harvested plot was rich in DON while the forest floor in an adjacent whole-tree harvested plot had no detectable DON (Stevens and Wannop 1987). This suggests that the removal of logging slash during whole-tree harvesting eliminated an important source of soluble organic N. Residual fine roots would have remained in forest soil after both conventional and whole-tree harvesting. Thus, fine roots are less likely to be an important source of SON than slash in these forests. Qualls et al. (2000) found that logging slash from an Appalachian deciduous forest was three times richer in DON than throughfall from an undisturbed forest.

If logging slash causes temporary increases in the concentrations of SON and DON, the differences between clearcuts and forest may increase as soluble organics from logging slash are depleted. Indeed, Chang et al. (1995) found that SON concentrations were similar in H-layer forest floor material from old-growth forests and 3-year-old clearcuts, but that SON concentrations were lower (though not significantly) in 10-year-old clearcuts. However, DON and SON concentrations remained elevated in humus from a clearcut Norway spruce forest even 5 years after harvest (Smolander et al. 2001). Clearly, plant inputs are not the only sources of SON.

What other processes could be controlling the concentration of SON in forest soil?

There is some evidence to suggest that soil microbes can produce SON. Qualls et al. (1991) found that inorganic N deposited in the forest floor via throughfall was converted to DON prior to leaching into the mineral soil. In several studies it has been shown that ^{15}N-labelled nitrate or ammonium applied to forest soil appears rapidly in SON and DON pools (Van Cleve and White

1980; Seely and Lajtha 1997). This rapid conversion of N from inorganic to organic form has been attributed to microbial immobilization (Van Cleve and White 1980; Qualls et al. 1991; Seely and Lajtha 1997). Based on experiments in which the movement of N was tracked through temperate forest soils in Chile, Perakis and Hedin (2001) suggested that the microbial biomass is an important conduit for organic N, but a poor sink. Thus, N immobilized by soil microbes is probably rapidly released as SON when microbial cells turn over. Indeed, elevated concentrations of SON have been observed when microbial populations crash (Hart et al. 1994; Chapman et al. 2001).

In addition to producing SON by N immobilization and turnover, soil microbes may generate SON by decomposing larger organic molecules. Fungi release exoenzymes capable of mobilising N from a variety of complex organic substrates (Chalot and Brun 1998). In a laboratory study, an ericoid and an ectomycorrhizal fungus both released amino acids as a product of decomposition when grown with protein as their sole N-source (Langdale and Read 1989). In two Douglas-fir forests, Griffiths et al. (1994) found that the concentration of total dissolved N in soil solution was significantly higher in soils associated with ectomycorrhizal mats than in non-mat soils. Most of the total dissolved N measured in solution from these soils can be attributed to DON because nitrate and ammonium concentrations were very low.

If microbial production is an important pathway for the formation of SON, higher microbial populations should be associated with elevated SON concentrations. Several studies have found high concentrations of SON during periods of high soil moisture content (Van Cleve and White 1980; Williams 1992; Lipson et al. 1999). The common interpretation of this observation is that wet forest soils support larger populations of soil microbes, which in turn produce greater quantities of SON. A positive correlation was found between moisture content and microbial

biomass in a northern hardwood forest soil, but the relationship was not very strong (R^2 between 0.27 and 0.59; Taylor et al. 1999). When moisture content is kept constant during incubation of forest soil, SON concentrations have been shown to increase, decrease or remain the same (Schmidt et al. 1999; Smolander et al. 2001). Thus, it is not clear how microbial activity, SON production and soil moisture content are related.

Some studies suggest that soil microbes control the concentration of SON not by its production, but by its consumption. Although soil microbes are capable of assimilating both mineral N and organic N (Hadas et al., 1992), Qualls and Haines (1992) found that DON decomposed very slowly during an experiment to determine the biodegradability of dissolved organic material from throughfall and soil solution. However, the results of this experiment may have been biased because the activity of basidiomycetes was probably suppressed (Qualls and Haines 1992). Some species of basidiomycetes are capable of mobilising N from protein-polyphenol complexes (Bending and Read 1996), and such materials are common in DON from forest soil (Qualls and Haines 1991).

In support of the hypothesis that soil microbes actively degrade SON, investigators have found an inverse relationship between SON and SIN in some forest soils (e.g., Hart et al. 1994; Casals et al. 1995; Jones and Kielland 2002). This suggests that low concentrations of SON are caused by its mineralization to inorganic N. During laboratory incubations, the concentration of SON often declines as the concentration of SIN increases (Hart et al. 1994; Huang and Schoenau 1998). However, N mineralization did not completely explain decreased SON concentrations during incubation of soil from a pine forest in Spain (Casals et al. 1995) or upland and peatland forests in the Canadian Shield (Devito et al. 1999). In these studies, the concentration of SON in incubated soil occasionally declined more than the concentration of SIN increased.

Abiotic processes such as adsorption, precipitation, and physical transformation of one fraction to another probably play an important role in controlling the concentration of SON during soil incubation (Smolander et al. 2001). Chapman et al. (2001) found that the concentration of nitrate rose continuously during incubation of podsolic soil cores but the concentration of DON remained relatively constant. They hypothesized that organic N sorbed to soil particles was continuously released into the soil solution. Neff et al. (2000) proposed that physical processes such as sorption and desorption can be the dominant factors controlling the release of DON from some surface soil horizons.

Organic N can be abiotically adsorbed to organic and mineral soils by anion exchange, ligand exchange, cation bridging, hydrogen bonding and van der Waals forces (Greenland 1971; Kalbitz et al. 2000; Qualls 2000). Qualls (2000) showed that hydrogen bonding in forest floor from a *Pinus jeffreyi* stand and ligand exchange with iron and aluminum hydroxides in a fine-loamy Typic Hapludult were the most important processes of abiotic adsorption. Hydrophobic acids, generally a large fraction of DON, are particularly susceptible to adsorption on mineral soil particles (Qualls and Haines 1991). In lodgepole pine forests in Wyoming, it was estimated that finer-textured surface mineral soils retained up to 0.1 g organic N/m^2 during snowmelt each year (Fahey et al. 1985).

Adsorption of organic N to mineral soil particles may be an important mechanism for the retention of nutrients after disturbance. Borchers and Perry (1992) found that coarser soil had lower total C and N concentrations prior to timber harvesting, and released a greater proportion of total sorbed N following timber harvesting. After logging a Douglas-fir forest in Oregon, Sollins and McCorison (1981) measured elevated concentrations of DON below the rooting zone (*i.e.*, below 2 m). Although they were not certain of the mechanism by which this would occur,

they hypothesized that forest disturbances trigger desorption of large quantities of previously sorbed organic N and loss of this N in leachate.

How do these processes affect the vertical distribution of SON in the soil?

Concentrations of DON and SON are highest at the soil surface (e.g., Bauhus 1998; Huang and Schoenau 1998; Michalzik and Matzner 1999). Elevated concentrations of SON at the surface of the forest floor are probably the result of fresh inputs of organic N-rich litter and throughfall (Chang et al. 1995; Bauhus 1998; Huang and Schoenau 1998). Fine roots (Vogt et al. 1981; Persson et al. 1995; Makkonen and Helmisaari 1998) and soil microbes (Fritze et al. 2000; Ekelund et al. 2001; Nikonov et al. 2001) may contribute to this pattern because they are also concentrated in surface soil horizons.

As water percolates down the soil profile, the concentration of DON generally declines (Sollins and McCorison 1981; Michalzik and Matzner 1999). Several interacting processes probably contribute to this pattern. Some organic N is probably lost to mineralization (Sollins and McCorison 1981; Qualls and Haines 1992) or plant uptake (e.g. Sollins and McCorison 1981; Finlay et al. 1992; Nasholm et al. 1998). However, abiotic adsorption is probably the strongest sink for organic N percolating through forest soil because it can occur very rapidly and because DON seems to mineralize very slowly (Sollins and McCorison 1981; Qualls and Haines 1991; Michalzik and Matzner 1999).

In experiments where concentrations of SON were expressed as a function of soil mass, SON in the mineral soil was between 2 and 50% of the SON in the forest floor (Bauhus 1998; Huang and Schoenau 1998). Given that forest floor and mineral soil have very different bulk densities, SON

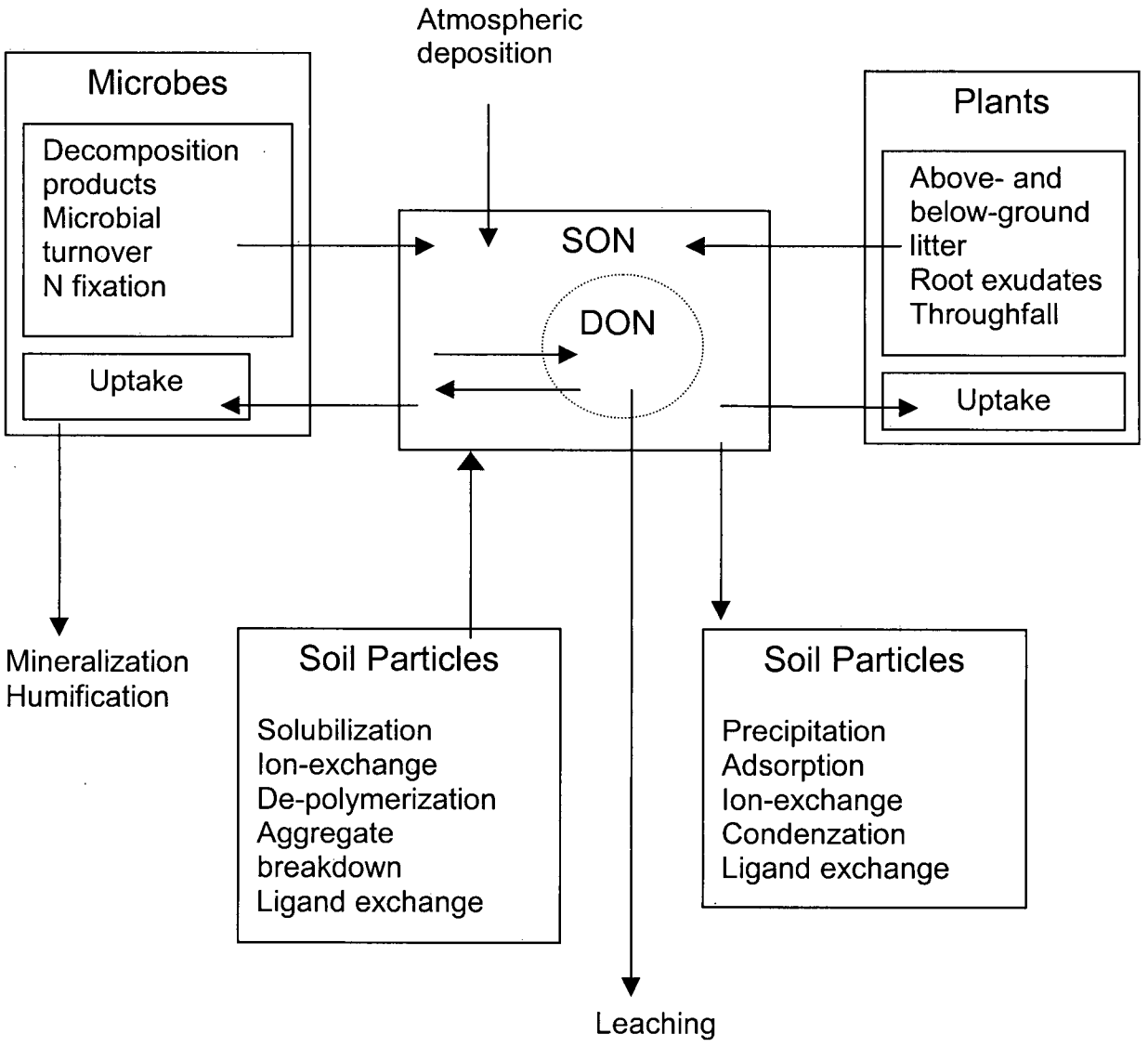

Figure 1. Sources and sinks for soluble organic N and dissolved organic N in forest soils.

concentrations in forest floor and mineral soil are best compared when expressed on a volume of soil basis. Differences between forest floor and mineral soil in the concentration of SON, which includes some previously sorbed material, are especially interesting because they may reflect differences in abiotic retention of organic N.

The amino acid fraction of SON

Amino acids are the building blocks of proteins and are the most abundant N-containing constituents of living organisms. Plant litter and roots are important sources of amino acids, either directly in throughfall and root exudates (Bowen 1969; Grayston et al. 1996), or indirectly in decomposing litter (Abuarghub and Read 1988b; Langdale and Read 1989; Kielland 1995). Although free amino acids typically make up only a small fraction of SON (Turnbull et al. 1995; Schmidt and Stewart 1997; Jones and Kielland 2002), they appear to turn over rapidly (Putnam and Schmidt 1958; Jones 1999; Jones and Kielland 2002).

As previously mentioned, the results of several studies suggest that plants can take up organic N intact, at least when it is in amino acid form. High ratios of ^{13}C to ^{15}N from double-labelled amino acids were found in plant tissues after the injection of these substrates into soil with growing plants. This indicates that the amino acids were not mineralized prior to uptake (Nasholm et al., 1998; Nasholm 2000; Nordin et al., 2001). Laboratory experiments have found evidence for one or more active amino acid transport mechanisms in roots of castor bean (*Ricinus communis*) and corn (*Zea mays*) (Schobert and Komor 1987; Schobert et al. 1988; Jones and Darrah 1994).

The uptake of amino acids by plants and soil microbes may reflect several competing factors. In a number of studies, microbial uptake was slowest for amino acids with a low C:N ratio

(Kielland 1994; Lipson et al. 1999; Raab et al. 1999). Using substrate-induced respiration and most probable number techniques, Lipson et al. (1999) found that glutamate supported greater microbial population growth than glycine, and suggested that this was due to the higher C:N ratio of glutamate. Because competition from soil microbes may be less intense for amino acids with lower C:N ratios, these amino acids may be more available for uptake by plants (Lipson et al. 1999).

The C:N ratio of individual amino acids is not the sole factor determining their availability (Jones and Hodge 1999; Jones and Kielland 2002). Lysine, a basic amino acid, is more susceptible to adsorption than other neutral or acidic amino acids (Jones and Hodge 1999; Vinolas et al. 2001b). Neutral amino acids readily diffuse in soil solution, and acidic amino acids tend to dissolve because they exist primarily as anions (Kielland 1994; Lipson and Nasholm 2001; Vinolas et al. 2001b). In contrast, basic amino acids carry a positive charge in acid soils. This allows them access to cation exchange sites (Kielland 1994; Lipson and Nasholm 2001; Vinolas et al. 2001b). As a result, with the exception of arginine, basic amino acids are generally the least abundant free amino acids in soil extracts (Table 2).

Abiotic adsorption effectively competes with soil microbes for amino acids. Vinolas et al. (2001b) found that the mineralization rate of individual amino acids applied to mineral soil was negatively correlated with sorption strength. In addition, the decomposition rate of amino acids declined dramatically when they were complexed with humic polymers (Verma et al. 1975). The role of adsorption in the availability of amino acids in soil may have been underestimated in the past. When amino acids were added to an alpine soil, up to 75% were abiotically retained in the non-biomass soil fraction (Lipson and Monson 1998; Raab et al. 1999). Abiotic adsorption of

amino acids may be especially important in organic soils, although the mechanism of this retention is not well understood (Raab et al. 1999).

Table 2. The most abundant free amino acids detected in water extracts of soils or in soil solution. Numerical values are given when possible. Dots (•) indicate the most abundant amino acids when numerical values were not provided.

	Net charge	Water extracts of soil (μg/g)					Soil solution (μg/ml)	
		Ivarson & Sowden (1966)	Kielland (1995)	Turnbull et al. 1995	Schmidt & Stewart 1997	Nordin et al. 2001	Dadd et al. 1953	Raab et al. 1999
		Temperate forest	Arctic tundra	Eucalypt forest	Subtropical heath	Boreal forest	Deciduous woodland	Alpine/ subalpine
Alanine	0	0.015	-	•	•	0.09-0.62	0.8	-
Arginine	+1	-	0.2-1.8	-	-	0.01-0.26	-	-
Asparagine	0	-	-	-	-	0.03-0.54	-	-
Aspartic Acid	-1	-	0.05-0.8	•	•	-	0.6	•
Glutamic Acid	-1	0.02	0.02-0.7	-	•	-	0.6	•
Glutamine	0	-	-	-	-	0.07-1.79	-	-
Glycine	0	-	0.05-0.7	•	•	0.06-0.30	0.6	•
Leucine	0	0.015	0.05-0.15	•	-	-	-	-
Serine	0	0.015	0.03-2.9	•	•	0.08-0.34	0.6	-
Threonine	0	0.015	0.01-0.9	-	-	-	-	-
Valine	0	0.02	-	-	-	-	-	-

Given that plants can take up amino acids directly, their abundance in forest soil is of interest. Free amino acids have been measured in many studies (Table 2), but the results of these studies must be interpreted with caution because different extractants were used. The quantity of free amino acids measured in soil extracts is highly dependent on the method of extraction (Sowden and Ivarson 1966; Ivarson and Sowden 1969; Abuarghub and Read 1988a). The lowest amino acid concentrations are found in water extracts. Water extracts probably best represent free amino acid concentrations under field conditions (Ivarson and Sowden 1969). However, they provide only a conservative estimate of the amino acids available for uptake because amino acids

are rapidly adsorbed on soil particles and metabolized by soil microbes (Raab et al. 1999; Vinolas et al. 2001b).

Free amino acid concentrations are generally below 100 μg/g, and amino acids in water extracts rarely exceed 20 μg/g (Table 3). There are no obvious differences in the concentrations of amino acids in forest floor and mineral soils, nor are there clear differences between forest and non-forest soils. There appear to be no published studies addressing the effects of timber harvesting on the abundance of amino acid-N in soil.

Table 3. Summary of studies of free amino acids in soil. Some values have been calculated from information given in the paper or have been estimated from graphs.

Ecosystem	Country	Extract	Soil type or horizon	Amino acid concentration	Citation
Various ecosystems	England	Solution squeezed from soil	Peat	3.4 μg N/ml	Dadd et al. (1953)
			Sphagnum litter	1.2 μg N/ml	
			Humus from oak woodland	4.8 μg N/ml	
Pine forest	Norway	Ether and water	Air-dried F-layer forest floor	0.074% of dry organic matter	Grov (1963)
			Air-dried H-layer forest floor	0.14% of dry organic matter	
			Air-dried A horizon mineral soil	0.52% of dry organic matter	
Various locations near Ottawa	Canada	Methanol	Ah horizon of clay loam brown forest soil	0.16 μg/g	Ivarson & Sowden (1966)
			H-layer from sandy loam podsolic soil	0.12 μg/g	
			0-6 cm peat	1.04 μg/g	
Various locations near Ottawa	Canada	CCl_4	Ah horizon of clay loam brown forest soil	144.2 μg/g	Sowden & Ivarson (1966)
			H-layer from sandy loam podsolic soil	105.6 μg/g	

Table 3. (continued)

Ecosystem	Country	Extract	Soil type or horizon	Amino acid concentration	Citation
Podsolic soil	Quebec, Canada	Weak HCl	0-15 cm mineral soil	4.4 μg/g	Warman & Bishop (1987)
		10% ethanol		22.6 μg/g	
Calluna heathland	England	NH_4OAC	Litter	41-299 μg/g	Abuarghub et al. (1988a)
			0-5 cm mineral soil	10-84 μg/g	
			5-10 cm mineral soil	6-62 μg/g	
Deciduous forest	Germany	Electro-ultrafiltration	Upper horizon of sandy soil	5.3 μg N/g	Nemeth et al. (1988)
Pine forest			Upper horizon of loamy sand soil	8.0 μg/g	
Dry heath	Alaska, United States	Water	0-10 cm of organic horizon	1-6 μg N/g	Kielland (1995)
Wet meadow				1-2.5 μg N/g	
Tussock tundra				2.5-18 μg N/g	
Shrub tundra				1-6 μg N/g	
Eucalyptus forest	Australia	Water	0-5 cm mineral soil	3.4 nmol N/g	Turnbull et al. (1995)
Subtropical wet heathland	Australia	Water	0-5 cm mineral soil	2 ng N/g	Schmidt & Stewart (1997)
Alpine meadow	Colorado, United States	Soil pore water collected in lysimeters	Lysimeters buried 10 cm deep in the A horizon	0-158 μmol/L	Raab et al. (1999)
Subalpine fen				0-75 μmol/L	
Shortgrass steppe				0-200 μmol/L	
Dwarf shrub forest	Sweden	Water	Mor forest floor	1.5-4 μg N/g	Nordin et al. (2001)
Tall-herb forest				0.5-7 μg N/g	
Low-herb forest				0.5-2 μg N/g	

OBJECTIVES

This study will address several questions pertaining to the quantities of SON and amino acid-N in forest soil and the impact of timber harvesting on their abundance:

1) **Is SON more abundant in forest soil than SIN?** SON is the dominant form of soluble N in most forest soils but it is unknown if this is true in B.C. forests, which are typically considered N-limited.

2) **Is the content of SON in the top 20 cm of forest soil different in forests and clearcuts?** The effects of timber harvesting on SON are difficult to predict. Variable results have been reported in the few studies examining differences in SON concentration between forests and clearcuts. Post-harvest changes in SON, especially in the top 20 cm of forest soil where the roots of young seedlings are concentrated, may have implications for reforestation.

3) **Is the concentration of SON in forest soil related to moisture content and its effects on microbial activity?** Changes in SON concentration have been attributed to changes in soil moisture and its control over microbial activity. A positive correlation between microbial biomass and moisture content has been found in some forest soils, but other factors, such as adsorption on soil particles, may more strongly control the concentration of SON.

4) **What happens to SON during *in situ* incubation?** SON concentrations can increase, decrease or stay the same during field incubation, and both biotic and abiotic processes can control these changes.

5) **Does SON concentration (on a per volume basis) vary among forest floor and mineral soil layers?** Differences in SON concentration between soil types may reflect differences in their ability to abiotically retain organic N because SON includes some previously adsorbed organic N. According to previous studies, the concentration of SON is usually much higher

in the mineral soil than in the forest floor. However, comparisons of forest floor and mineral soil layers may have been confounded by differences in bulk density.

6) **Is amino acid-N the dominant form of SON? Does amino acid-N show the same patterns as SON?** SON is composed of numerous types of organic molecules. Amino acids are typically a small portion of SON. The quantity and distribution of amino acids in forest soil, and the impact of forest harvesting on their abundance, are of interest.

MATERIALS AND METHODS

Research sites

Three pairs of clearcuts adjacent to old-growth forests were selected at two study sites. Both sites were already the subjects of extensive research examining the impact of forestry activities on nutrient cycling and forest regeneration.

The Salal Cedar Hemlock Integrated Research Program (Prescott and Weetman 1994) site is located near Port McNeill B.C., in the very wet maritime subzone of the Coastal Western Hemlock (CWHvm) biogeoclimatic zone (Green and Klinka 1994). This site will be referred to as 'Port McNeill'. The forest is a mix of western redcedar (*Thuja plicata* Donn.) and western hemlock (*Tsuga heterophylla* (Raf. Sarg.)) with a thick shrub layer of salal (*Gaultheria shallon* Pursh) and *Vaccinium* spp. Topography is gently rolling; elevations are less than 300 masl. 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 with a 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).

Previous studies at Port McNeill have addressed the poor regeneration and growth observed on clearcuts in this area. For the present study, three blocks were selected, each consisting of an uncut old-growth forest and an adjacent operationally-harvested clearcut. Clearcuts were selected with as similar an age and site history as possible. Clearcuts in Block 1 (50° 36'N 127° 22'W) and Block 2 (50° 34'N 127° 17'W) were 98.5 ha and 67.0 ha, respectively. Both were

harvested in 1994/95 and prescribed burned in 1996. 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 clearcut in Block 3 (50° 39'N 127° 24'W), a 32.1 ha clearcut within a larger cutblock, was harvested in 1992/93, prescribed burned in 1993 and planted with western redcedar in 1994. Within each treatment unit, samples were collected from an area about 150 m by 150 m.

The Sicamous Creek Silvicultural Systems Trial (Vyse 1999) site is located near Sicamous B.C., in the wet cold subzone of the Engelmann spruce/Subalpine fir (ESSFwc) biogeoclimatic zone (Lloyd et al 1990). This site will be referred to as 'Sicamous'. This high-elevation (1550-1750 m) forest has a mix of Engelmann spruce (*Picea engelmannii* Parrry) 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 moderate (20-40%) slopes. Average precipitation during the growing season (measured at the Sicamous site from 1993 to 2000) is 308 mm. 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, personal communication). The snow-free period generally lasts from late June to early October. On mesic sites, mineral soils are well- to poorly-drained orthic Humo-Ferric Podzols with a sandy loam texture overlying morainal deposits (Hope 1997). Forest floors are thin (average 4-5 cm) and are predominantly hemimors (Green et al. 1993).

Previous studies have been established at Sicamous (50° 49'N 119° 54'W) to examine the long-term impact of harvesting in high-elevation forests in interior B.C. Prior to this study, the area had been divided into three blocks based on elevation. Within each block five treatments were

applied: uncut forest, single-tree selection, and 0.1 ha 1.0 ha and 10 ha clearcuts. The three 30 ha uncut forests and three 10 ha clearcuts were used in this study. Clearcuts were harvested in the winter of 1994/95 and were mounded but not burned prior to planting with Engelmann spruce in 1996. Within each treatment unit, samples were collected from an area about 30 m by 30 m.

Sample collection

Samples were collected haphazardly from each treatment unit at both sites. Sampling was confined to the top 20 cm of either forest floor (Port McNeill) or forest floor plus mineral soil (Sicamous) in order to characterize the seedling root environment. Seven samples were collected from each of the three clearcuts and three uncut forests at both sites. At Port McNeill, samples were collected every four weeks between June and September 1999 and between May and September 2000. In the uncut forest, separate samples of F- and H-layer forest floor were collected. Since there was little or no F layer in the clearcuts, only H-layer forest floor was collected. At Sicamous, samples were collected every four weeks from July to September in 1999 and 2000. Because the forest floor was thin, the upper 20 cm contained both mineral soil and forest floor.

Prior to sample collection, the top layer of fresh litter was removed. Below this, samples were carefully removed using a trowel and root saw, placed in thin, plastic bags and stored in a cooler with ice packs. At Port McNeill, F- and H-layer forest floor samples were placed in separate bags. At Sicamous, forest floor and mineral soil samples were placed in separate bags. An identical number of samples were incubated in buried bags in July and August 1999 and in July 2000 (Eno 1960). Soils were incubated *in situ* for approximately 4 weeks. All samples were

transported to the lab within 2 days of collection and stored at 4°C until extraction (a maximum of 5 days in 1999 and 3 days in 2000).

Forest floor bulk density was determined at Port McNeill in July 2000. Within each treatment unit, seven 15 cm by 15 cm samples were excavated to a depth of 20 cm, placed in plastic bags and transported to the laboratory. After sieving and homogenizing, each sample was weighed. A portion of the sample was dried for 24 hours at 105 °C to determine moisture content. Bulk density was calculated by dividing the dry weight of the sample (g) by the volume of the sample (cm^3). Bulk density data, measured using a similar technique in July 2000 for Sicamous, was provided by Graeme Hope (Regional Soil Scientist, BC Ministry of Forests, Kamloops Region).

Soluble Organic and Inorganic N

Immediately before extraction, each soil sample was sieved (4.7 mm) and homogenized. A 5 to 6 g (fresh weight) subsample was weighed, extracted in 50 mL of 1M KCl solution and shaken (on ice) on a mechanical shaker for one hour. Soil solids were allowed to settle at 4 °C for one hour and then gravity-filtered. Most samples required about half an hour for complete filtration, but some samples of H-layer forest floor from Port McNeill required up to 2 hours. In 1999, samples were gravity-filtered at room temperature through pre-leached Whatman no. 42 or Fisher Q2 filter paper. 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, which suggests that the temperature at which the samples were gravity filtered did not strongly affect the results. A portion of each sample was dried at 105°C for 24 hours to determine moisture content.

Extracts were stored at 4°C until all samples had been extracted and gravity-filtered (2-4 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 in the Soil Science laboratory at the University of British Columbia.

A modified persulphate solution was used to convert dissolved N in the filtered soil extract to nitrate (Ameel et al. 1993; Cabrera and Beare 1993; Yu et al. 1994). 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 re-weighed to determine evaporation loss and then diluted with 5 mL of distilled deionized water. Persulphate digests were analysed for total N as nitrate using the same autoanalyser. SON was calculated by subtracting the quantity of soluble inorganic N (nitrate + ammonium) in the extract from the quantity of total soluble N in the extract. Cabrera and Beare (1993) suggest 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 1M KCl.

Microbial N

To determine whether changes in SON were related to changes in the microbial N pool, 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 had been incubated *in situ* for four weeks. For each sample, approximately 10 g fresh weight of sieved soil was incubated under vacuum with chloroform for 5 days. Fumigated samples were extracted in 100 mL of 1M KCl and shaken on ice for one hour. 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 was not used in the 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 weight of sieved soil was extracted in 50 mL of distilled, deionized water and shaken (on ice) on a mechanical shaker for one hour. In order to avoid damaging the HPLC, samples were not extracted in 1M KCl solution (S. Silim, personal communication). After shaking, samples were gravity-filtered at 4°C through pre-leached 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.

Prior to sample purification, the frozen extracts 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 vapour trap (RVT4104). Residues were dissolved in 1 mL 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, MA, USA). Amino acids were separated using a 3.9x150 mm AccQ.Tag Column (Waters Chromatography, Milford, MA, USA) 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-amino-butyric acid, γ-amino-butyric acid, alanine, arginine, asparagine, aspartic acid, cysteine, glutamic acid, glutamine, glycine, histidine, methionine, isoleucine, leucine, lysine, phenylalanine, proline, serine, threonine, tyrosine and valine. Derivatizations and analyses were performed in the Botany Department at the University of British Columbia.

Statistical Analysis

Most ecological studies of soluble soil nutrients report concentrations by mass of soil. This 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.

Although soil samples were collected from both sites on several sampling dates, these individual dates do not count as replicates. Thus, treatments were replicated only three times for a total of six treatment units (*i.e.*, three clearcuts and three old growth forests) at each site. Mean concentrations and contents of SON, SIN and microbial N were calculated for each treatment unit on every sampling date. Overall means were then calculated as the average of all sampling dates for each treatment unit such that the overall n=3. Differences between the concentration of SON and SIN were examined by site and by soil type using two-tailed paired t-tests. To examine treatment differences in SIN and SON content (kg/ha) and concentration ($\mu g/cm^3$), data were analysed using one-way ANOVA in a split (year) –split (month) randomized complete block design (Table 4). At Port McNeill, where samples were collected 3 times in 1999 and 5 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 (Table 5). Treatment differences in amino acid-N content (g/ha) and concentration (ng/cm^3) were analysed using one-way ANOVA in a randomized complete block design because amino acid-N was measured on only one date. The same ANOVA was used to analyze treatment differences in SON, SIN and microbial N concentrations and contents on individual sampling dates. Where necessary, data were log-transformed to meet the assumptions of normality and homogeneity of variance. Differences were considered significant at $p<0.05$.

To examine the relationships between moisture content, SIN, SON and microbial N, Pearson

correlations were calculated by site and soil type. 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 at $p<0.05$. All statistical analyses were performed using SAS (version 6.12, SAS Institute Inc. 1998, Cary, N.C.).

Table 4. Split-split randomized complete block design used to determine treatment differences in SON and SIN content and concentration at Sicamous.

Source of Variation	Degrees of Freedom	Mean Squares	F
Block	3-1=2	MS_B	MS_B/MS_{SE}
Treatment	2-1=1	MS_{Tr}	MS_{Tr}/MS_{E1}
Block x Treatment (Error 1)	(3-1)(2-1)=2	MS_{E1}	MS_{E1}/MS_{SE}
Year	2-1=1	MS_Y	MS_Y/MS_{E2}
Year x Treatment	(2-1)(2-1)=1	MS_{YTr}	MS_{YTr}/MS_{E2}
Error 2	2(3-1)(2-1)=4	MS_{E2}	MS_{E2}/MS_{SE}
Month	3-1=2	MS_M	MS_M/MS_{E3}
Month x Year	(3-1)(2-1)=2	MS_{MY}	MS_{MY}/MS_{E3}
Month x Treatment	(3-1)(2-1)=2	MS_{MTr}	MS_{MTr}/MS_{E3}
Month x Year x Treatment	(3-1)(2-1)(2-1)=2	MS_{MYTr}	MS_{MYTr}/MS_{E3}
Error 3	(2x2)(3-1)(3-1)=16	MS_{E3}	MS_{E3}/MS_{SE}
Sampling Error	(3x2x2x3)(7-1)=216	MS_{SE}	
Total	(3x2x2x3x7)-1=251	MS_T	

Table 5. Split randomized complete block design used to determine treatment differences in SON and SIN content and concentration at Port McNeill.

Source of Variation	Degrees of Freedom	Mean Squares	F
Block	3-1=2	MS_B	MS_B/MS_{SE}
Treatment	2-1=1	MS_{Tr}	MS_{Tr}/MS_{E1}
Block x Treatment (Error 1)	(3-1)(2-1)=2	MS_{E1}	MS_{E1}/MS_{SE}
Date	8-1=7	MS_D	MS_D/MS_{E2}
Date x Treatment	(8-1)(2-1)=7	MS_{DTr}	MS_{DTr}/MS_{E2}
Error 2	2(3-1)(8-1)=28	MS_{E2}	MS_{E2}/MS_{SE}
Sampling Error	(3x2x8)(7-1)=288	MS_{SE}	
Total	(3x2x8x7)-1=335	MS_T	

RESULTS

Is SON more abundant than SIN?

The concentration of SON ($\mu g/cm^3$) was significantly greater than that of SIN (Table 6) in every mineral soil and forest floor layer sampled. SON content on an areal basis (kg/ha) was also significantly greater than SIN content (Figure 2) in forests and clearcuts at both Port McNeill (p=0.0296 & .p=0.0136, respectively) and Sicamous (p=0.0058 & p=0.0056, respectively). 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, organic N remained the dominant form of soluble N.

Table 6. Concentrations of soluble organic N (SON) and soluble inorganic N (SIN) in the top 20 cm of forest soil at Port McNeill (forest floor only) and Sicamous (forest floor + mineral soil). Each value is the mean of three blocks, with standard deviation in parentheses. Differences were considered significant at $p<0.05$.

Site	Treatment	Soil	Concentration ($\mu g/cm^3$)			
			SON	SIN	p	Ratio
Port McNeill	Forest	F-layer	7.7 (1.1)	0.4 (0.05)	0.0187	19.3
		H-layer	4.5 (0.9)	0.2 (0.04)	0.0349	22.5
	Clearcut	H-layer	3.8 (0.4)	0.2 (0.02)	0.0140	19.1
Sicamous	Forest	Forest Floor	13.9 (1.6)	1.2 (0.5)	0.0091	11.8
		Mineral Soil	10.9 (0.4)	1.3 (0.7)	0.0078	8.0
	Clearcut	Forest Floor	6.9 (0.7)	2.7 (1.0)	0.0075	2.7
		Mineral Soil	9.3 (0.2)	1.8 (0.5)	0.0068	5.1

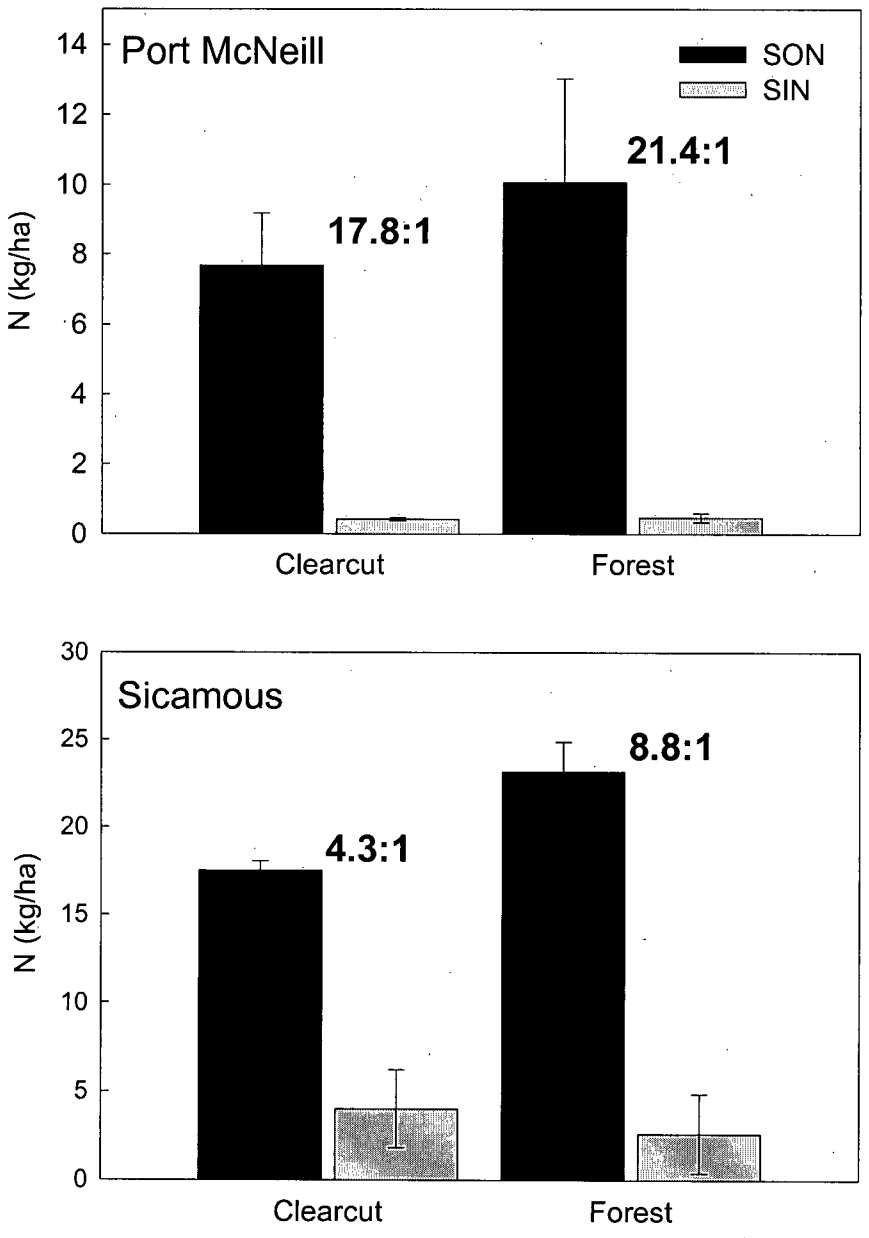

Figure 2. Contents of soluble organic N (SON) and soluble inorganic N (SIN) (kg/ha) in the top 20 cm of forest soil at Port McNeill (forest floor only) or Sicamous (forest floor + mineral soil) in clearcuts and forest. Each value is the mean of three blocks. Error bars indicate one standard deviation. The ratio of SON to SIN is shown above the data for each treatment.

Is SON content different in forests and clearcuts?

There were more consistent differences between forests and clearcuts in SON content than in SIN content. At both sites, SON content (kg/ha) tended to be lower in the clearcuts than in the forests (Figure 2). These differences were significant (p=0.0297) at Sicamous but not at Port McNeill. SIN content tended to be higher in the clearcuts than in the forests at Sicamous, and similar in clearcuts and forests at Port McNeill. Differences in SIN content were not significant at either site.

SON content also tended to be higher in the forests than in the clearcuts on individual sampling dates at both sites (except at Sicamous in September, 2000). However, differences between forests and clearcuts at Port McNeill were never significant (Figure 3). At Sicamous, SON content was significantly higher in the forests than in the clearcuts (p=0.0413) only in August 1999 (Figure 3) but were nearly significant in July 1999 (p=0.0597). SIN content was variable at both sites (Figure 4), and differences between forests and clearcuts were never significant.

The strength of differences between forests and clearcuts varied among forest floor and mineral soil layers. At Sicamous, the concentration of SON in the forest floor was significantly greater in forests than in clearcuts in July, August and September 1999 and in July, August and September 2000 (p=0.0139, 0.0282, 0.0205, 0.0113, 0.0272 & 0.0070, respectively). Differences in SON concentration between forests and clearcuts were never significant in the mineral soil (Figure 5), although differences were nearly significant in August 1999 (p=0.0643). At Port McNeill, the concentration ($\mu g/cm^3$) of SON was similar in H-layer forest floor from clearcuts and forests (Figure 6). Differences between forests and clearcuts in the concentration of SON in the F layer could not be compared because there was no F layer in the clearcuts.

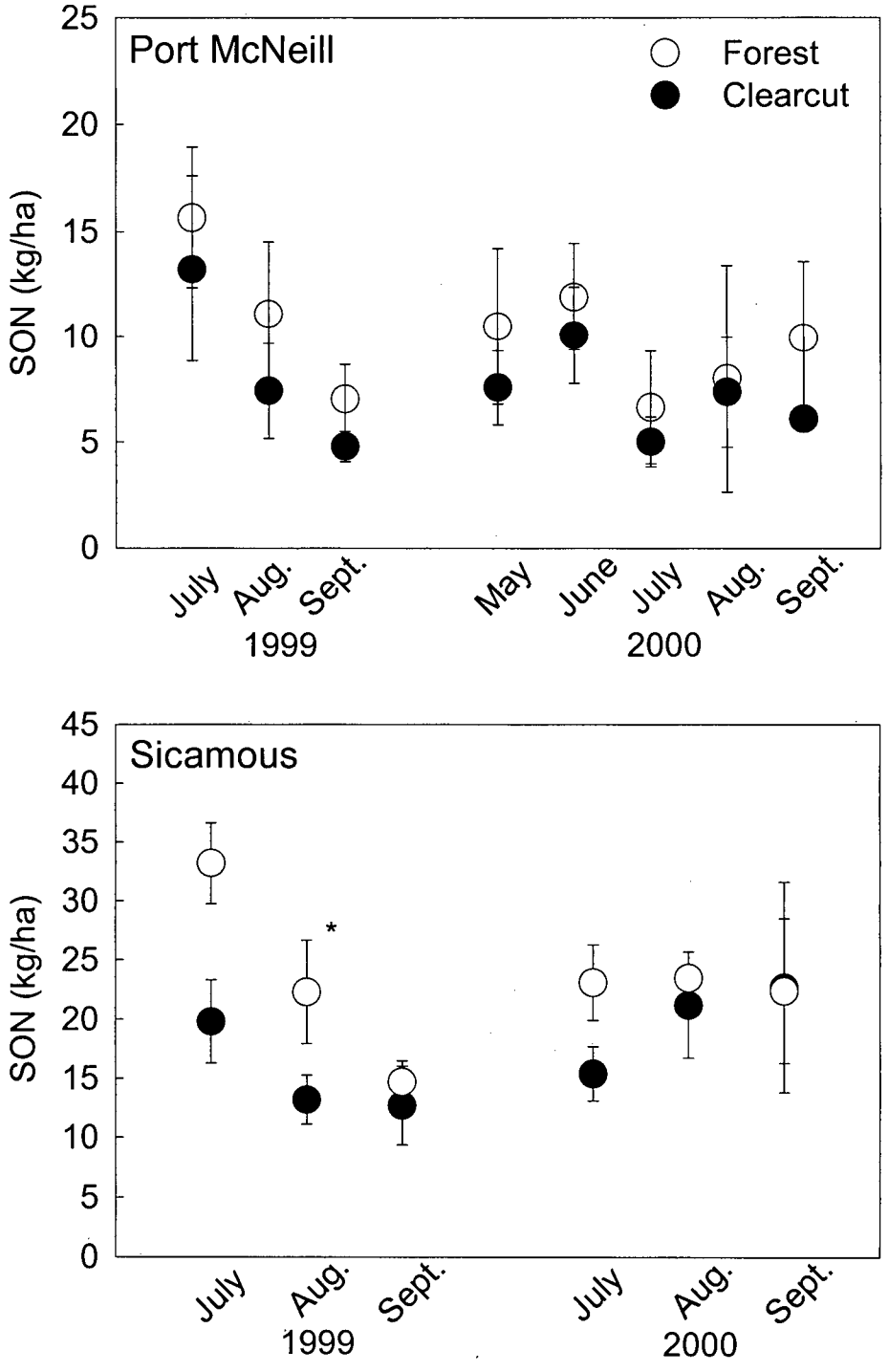

Figure 3. Content (kg/ha) of soluble organic N (SON) in the top 20 cm of forest soil at Port McNeill (forest floor only) and Sicamous (forest floor + mineral soil) in clearcuts and forests. Each value is the mean of three blocks. Error bars indicate one standard deviation. Asterisks indicate a significant difference between treatments at $p<0.05$.

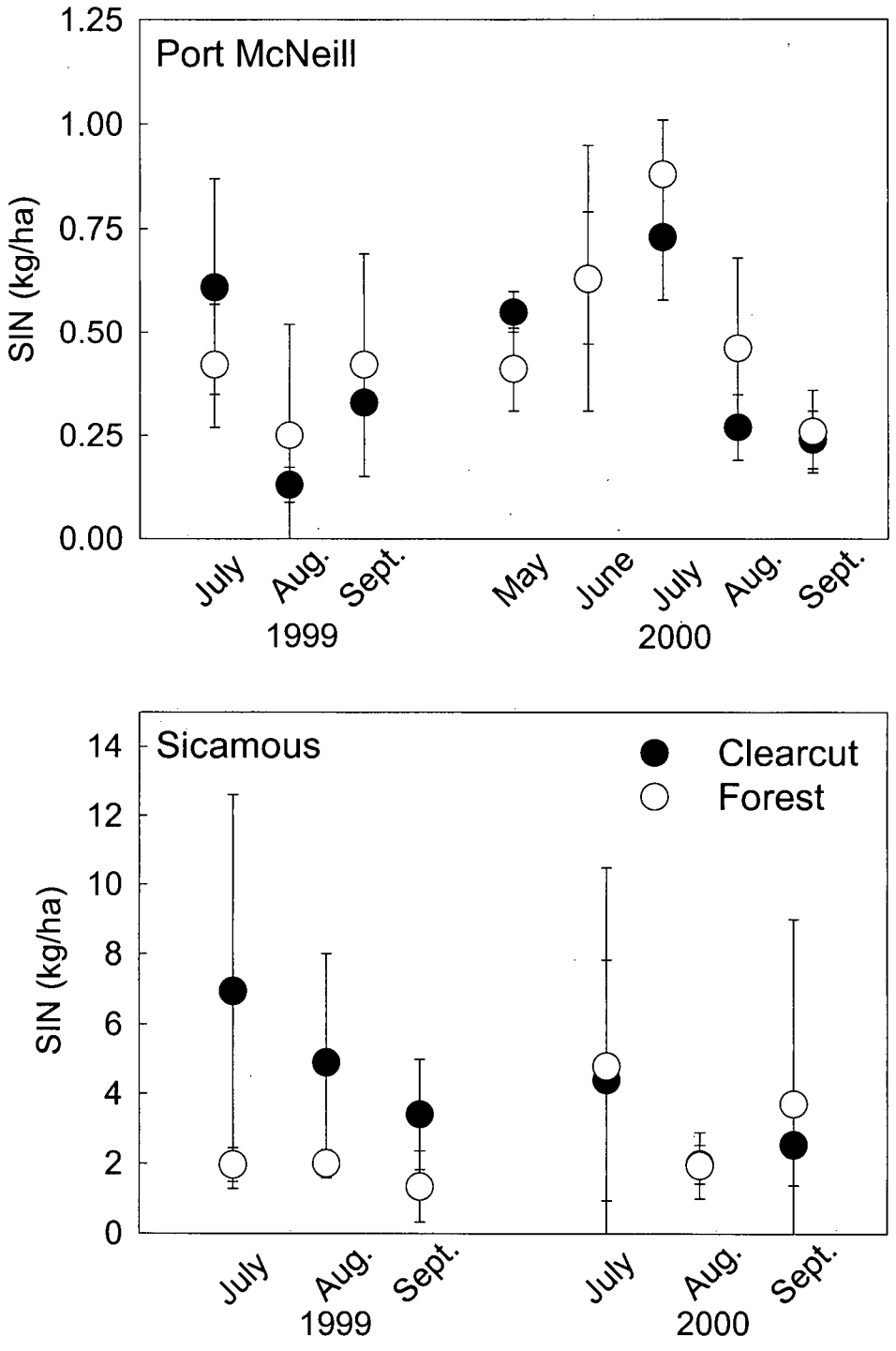

Figure 4. Content (kg/ha) of soluble inorganic N (SIN) in the top 20 cm of forest soil at Port McNeill (forest floor only) and Sicamous (forest floor + mineral soil) in clearcuts and forests. Each value is the mean of three blocks. Error bars indicate one standard deviation. Differences between forests and clearcuts on individual sampling dates were not significant.

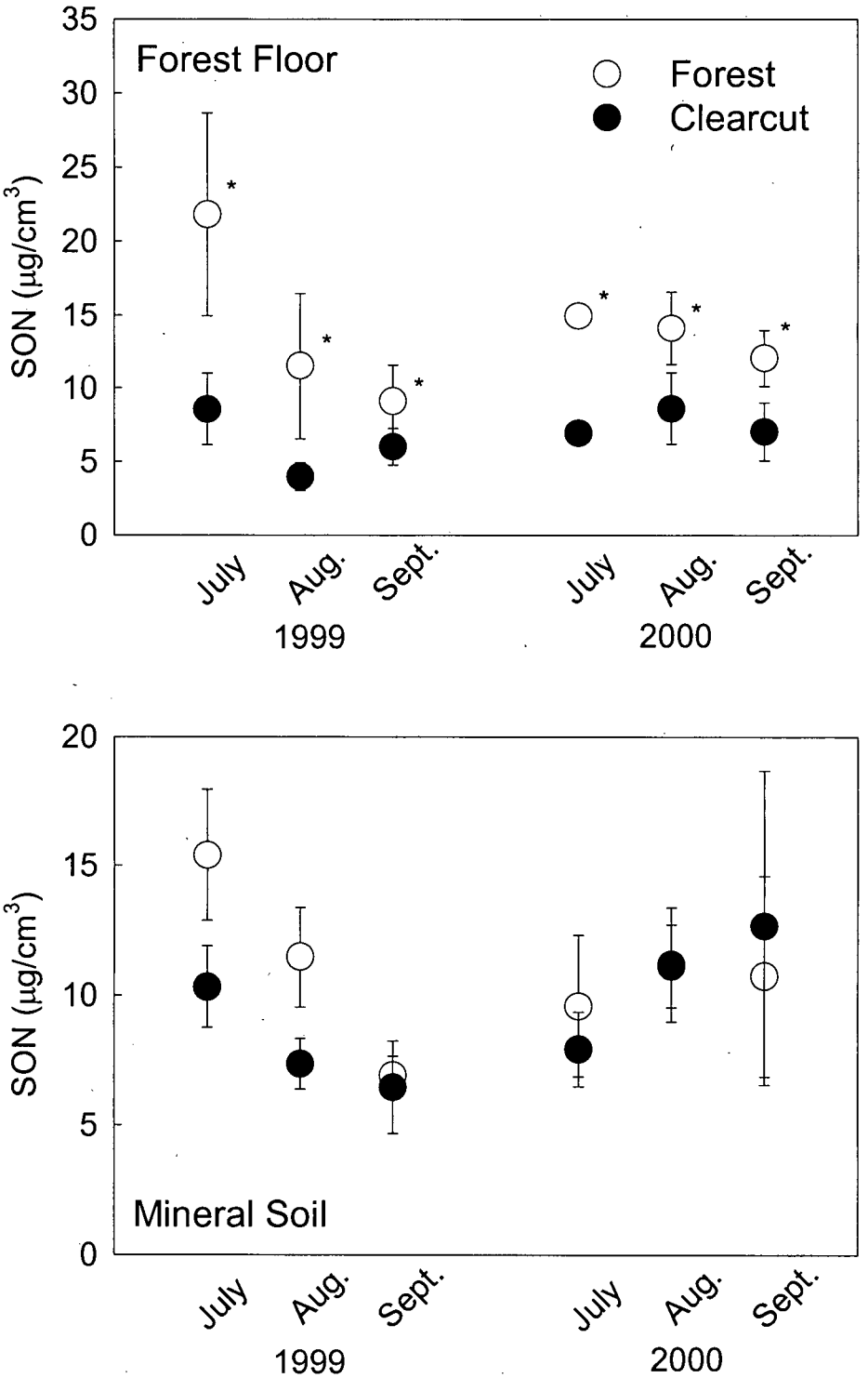

Figure 5. Concentration (µg/cm^3) of soluble organic N (SON) in the top 20 cm of forest floor and mineral soil in clearcuts and forests at Sicamous. Each value is the mean of three blocks. Error bars indicate one standard deviation. Asterisks indicate a significant difference between forests and clearcuts at $p<0.05$.

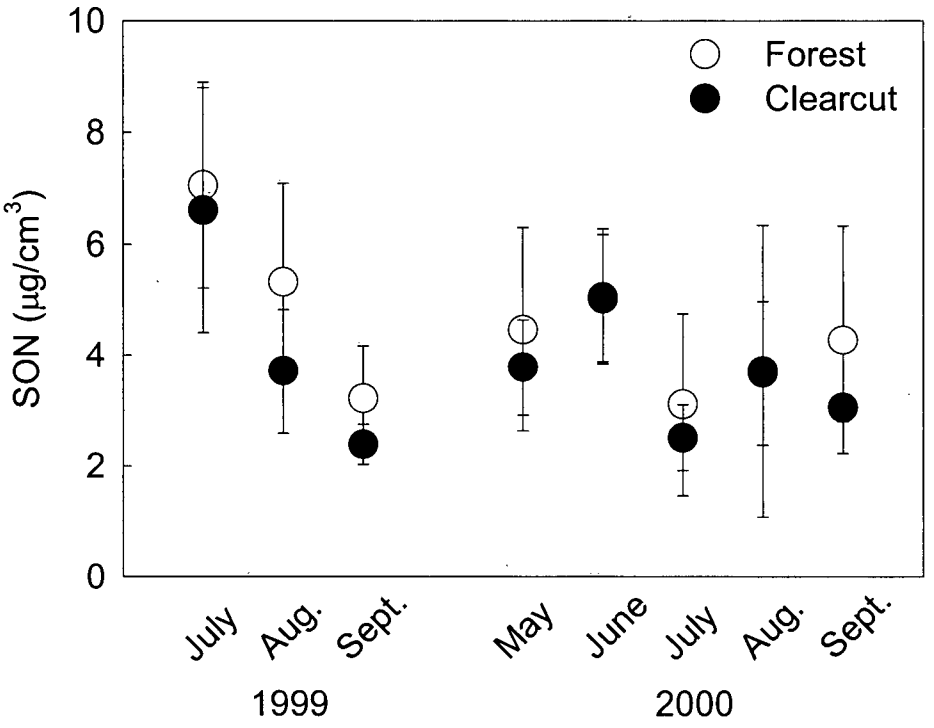

Figure 6. Concentration (µg/cm^3) of soluble organic N (SON) in H-layer forest floor in clearcuts and forests at Port McNeill. Each value is the mean of three blocks. Error bars indicate one standard deviation. Differences in SON concentration between forests and clearcuts on individual sampling dates were not significant.

What happens to SON during *in situ* incubation?

One-month buried bag incubations were used to examine short-term changes in concentrations of SON and SIN in the absence of litter and throughfall inputs, leaching losses and plant uptake. SON and SIN concentrations (µg/cm^3) in forest floor (Port McNeill and Sicamous) and mineral soil (Sicamous) showed similar changes after one-month incubation in July and August 1999 (Figure 7). 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 that of SIN at Port McNeill and was less than that of SIN in

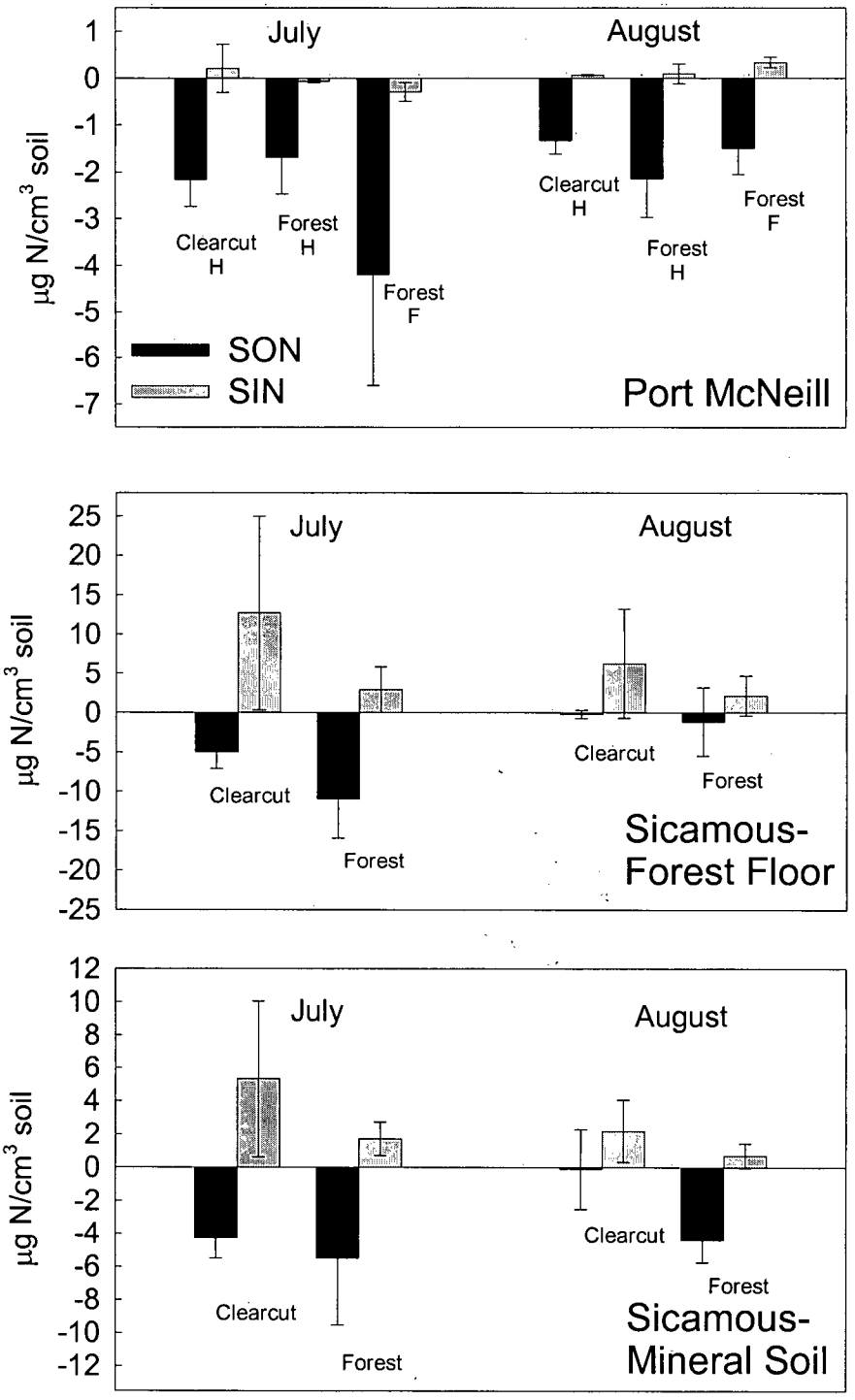

Figure 7. Net change in the concentrations ($\mu g/cm^3$) of soluble organic N (SON) and soluble inorganic N (SIN) at Port McNeill (forest floor only) and Sicamous (forest floor + mineral soil) during one-month buried bag incubations in July and August, 1999. Each value is the mean of three blocks. Error bars indicate one standard deviation.

the clearcuts at Sicamous. A third one-month incubation in July 2000 was used to determine if the decline in SON could be explained by microbial uptake. In contrast to the decline in SON observed after the July and August 1999 incubations, the concentration of SON increased during the third incubation (Figure 8). The only exception was the mineral soil from the forests at Sicamous, in which the concentration of SON declined. Contrary to expectations, average microbial N concentrations also increased during the third incubation in all soil layers at both sites.

Is the abundance of SON related to moisture content and its effects on microbial activity?

If moisture content controls the abundance of SON through its effects on microbial activity, close relationships between moisture content and the concentrations of microbial N, SON and/or SIN are expected. Soil moisture, SON and microbial N all tended to be highest in soil from the forests. At both sites, there were significant positive correlations between moisture content and SON and between moisture content and microbial N (Table 7). 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.

Does SON vary among forest floor and mineral soil layers?

At both sites, N concentrations differed in the forest floor and mineral soil layers examined (Figure 9). Microbial N was consistently more abundant than SON and SIN but there were no

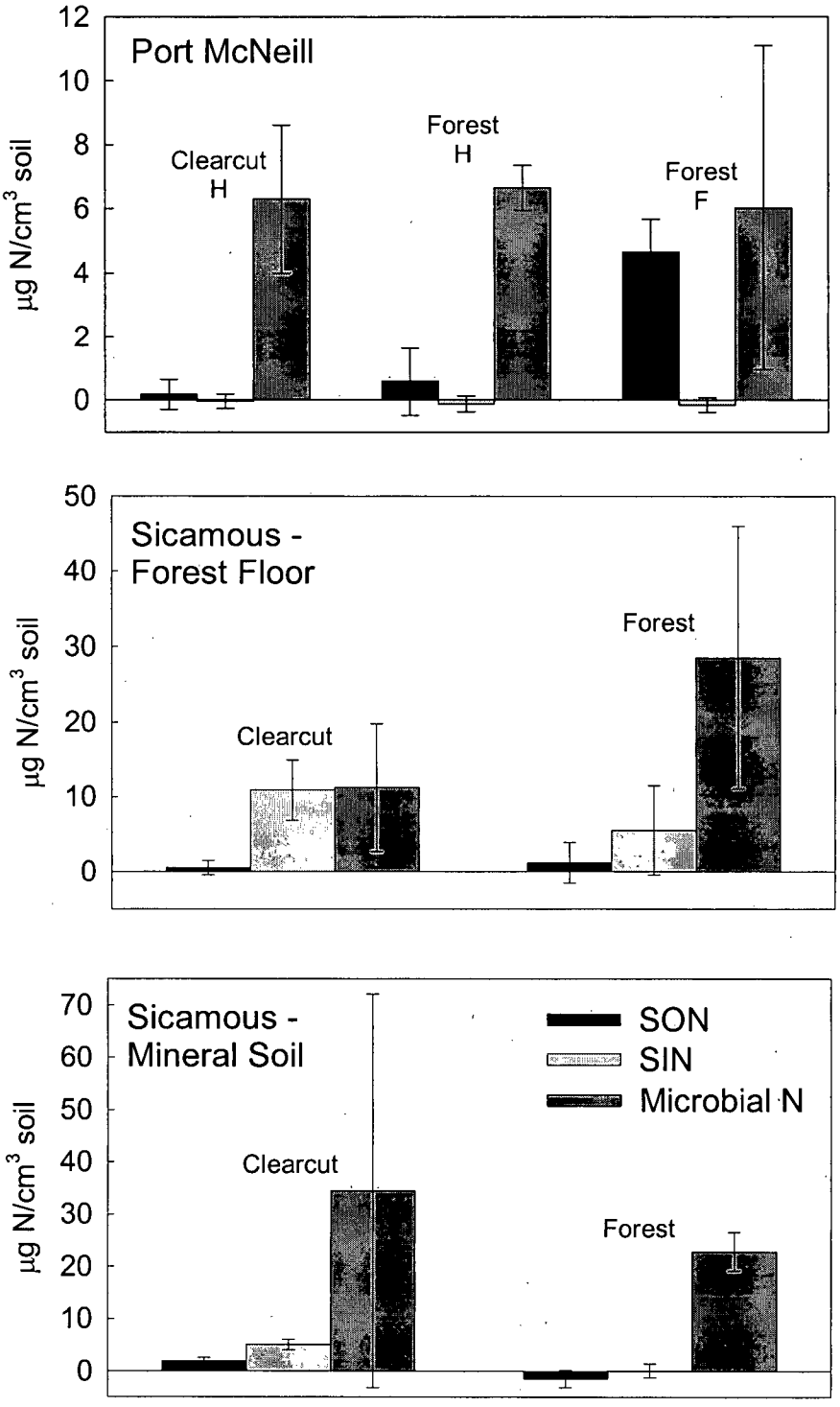

Figure 8. Net change in the concentrations ($\mu g/cm^3$) of soluble organic N (SON), soluble inorganic N (SIN) and microbial N at Port McNeill (forest floor only) and Sicamous (forest floor + mineral soil) during a one-month buried bag incubation in July 2000. Each value is the mean of three blocks. Error bars indicate one standard deviation.

Table 7. Results of correlation analyses a) between moisture content (cm^3 H_2O/cm^3 soil), and SON, nitrate-N, ammonium-N or microbial N concentration ($\mu g/cm^3$), and b) between SON concentration and nitrate-N, ammonium-N or microbial N concentration in the top 20 cm of forest soil at Port McNeill (forest floor only) and Sicamous (forest floor + mineral soil). Bold values indicate a significant relationship at $p<0.05$.

		Port McNeill				Sicamous			
		F-layer		H-layer		Forest floor		Mineral soil	
		r	*p*	r	*p*	r	*p*	r	*p*
a) Moisture content	SON	**0.323**	<0.001	**0.384**	<0.001	**0.366**	<0.001	**0.445**	<0.001
	NO_3^--N	0.045	0.562	0.029	0.604	0.022	0.730	-0.026	0.685
	NH_4^+-N	**0.406**	<0.001	**0.211**	<0.001	0.017	0.788	-0.039	0.537
	Microbial N	**0.909**	<0.001	**0.531**	<0.001	**0.386**	0.020	**0.440**	0.007
b) SON	NO_3^--N	-0.087	0.261	-0.009	0.877	-0.101	0.109	-0.017	0.784
	NH_4^+-N	**0.455**	<0.001	**0.209**	<0.001	0.019	0.761	0.047	0.456
	Microbial N	-0.097	0.702	0.303	0.072	**0.464**	<0.001	**0.638**	0.004

significant differences in microbial N between soil layers at either site. In the forests at Port McNeill, concentrations ($\mu g/cm^3$) of forest floor SON (p=0.0455) and SIN (p=0.0053) were significantly greater ($p<0.05$) in the F layer than in the H layer below. In the forests at Sicamous, SON concentrations ($\mu g/cm^3$) tended to be higher in the forest floor than in the mineral soil, but differences were not significant. Concentrations of SIN were similar in the forest floor and mineral soil. In the clearcuts at Sicamous, the concentration of SON in the forest floor tended to be less than that in the mineral soil, but differences were not significant.

Is amino acid-N the dominant form of SON? Does amino acid-N show the same patterns as SON?

In this study, SON and amino acid-N were extracted differently, so the pools cannot be directly compared. However, in a preliminary analysis water extracted approximately 35% of the SON

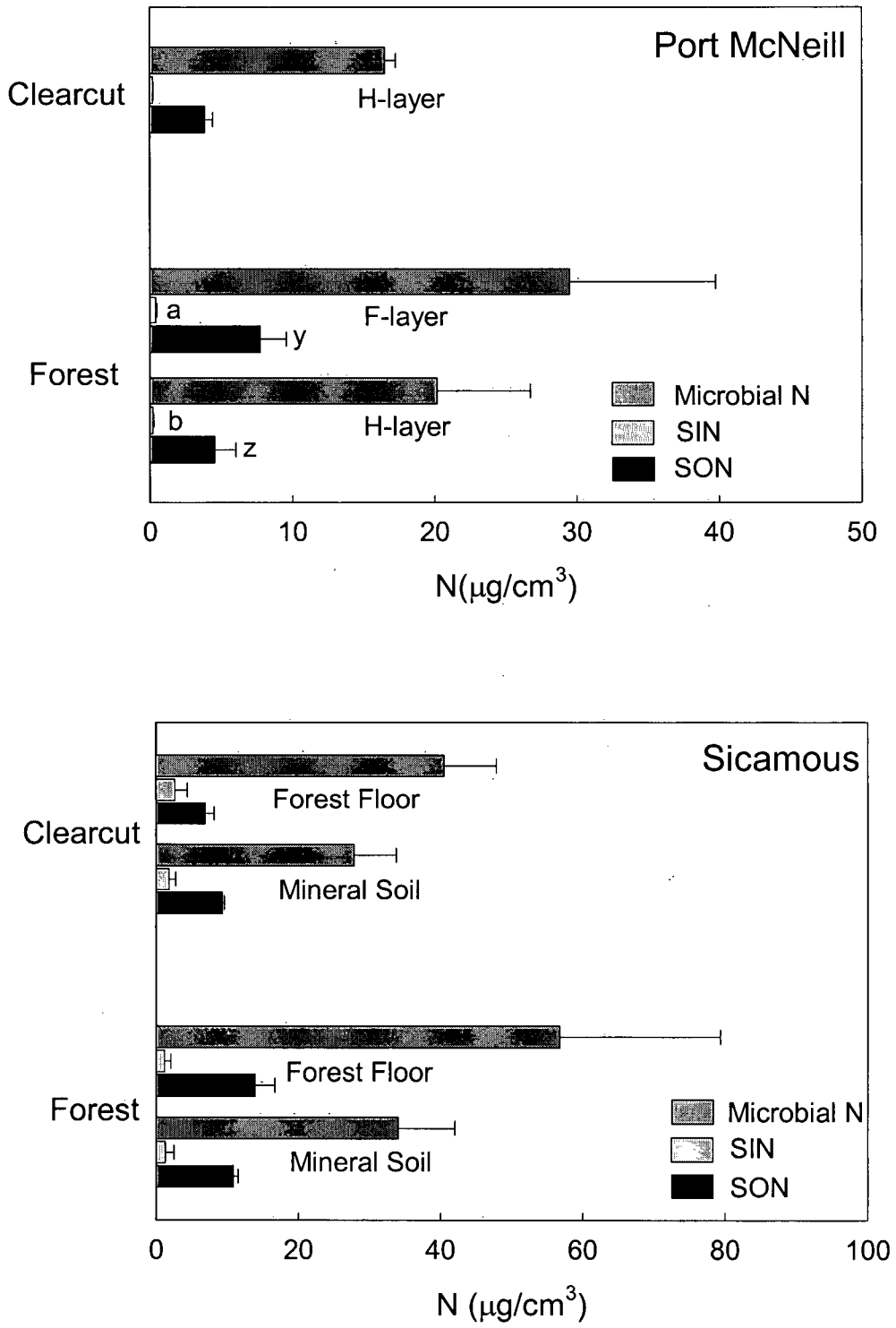

Figure 9. Concentrations ($\mu g/cm^3$) of microbial N, soluble inorganic N (SIN) and soluble organic N (SON) in each soil layer sampled from clearcuts and forests at Port McNeill and Sicamous. Each value is the mean of three blocks. Error bars indicate one standard deviation. Different letters indicate a significant difference between soil layers at $p<0.05$.

extracted by 1M KCl. Assuming that the composition of SON is similar in water and 1M KCl extracts, this indicates that about 1 to 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. At both sites, average amino acid-N content (g/ha) tended to be higher in forests than clearcuts (Table 8), but treatment differences were not significant.

Concentrations of amino acid-N were not significantly different in the forest floor and mineral soil layers examined. In the forests at Port McNeill, amino acid-N concentrations tended to be higher in the F- than in the H-layer forest floor. Concentrations of amino acid-N in H-layer forest floor from forests and clearcuts were similar (Figure 10). In the forest at Sicamous, amino acid-N concentrations tended to be higher in the mineral soil than in the forest floor (Figure 10). This pattern was not evident in the clearcuts, where amino acid-N concentrations were similar in the mineral soil and forest floor.

In every mineral soil and forest floor layer sampled, alanine and threonine were consistently among the five most abundant amino acids (Table 9). In addition, 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 from either forests or clearcuts. At Sicamous, arginine was abundant in forest floor from forests and clearcuts, and in mineral soil from the forest, but not in mineral soil from the clearcuts.

Table 8. Content (g/ha) of amino acid-N in the top 20 cm of soil in forests and clearcuts at Port McNeill and Sicamous. 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.

Site	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)

Table 9. Total amino acid concentrations (ng/cm^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. 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.

	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)

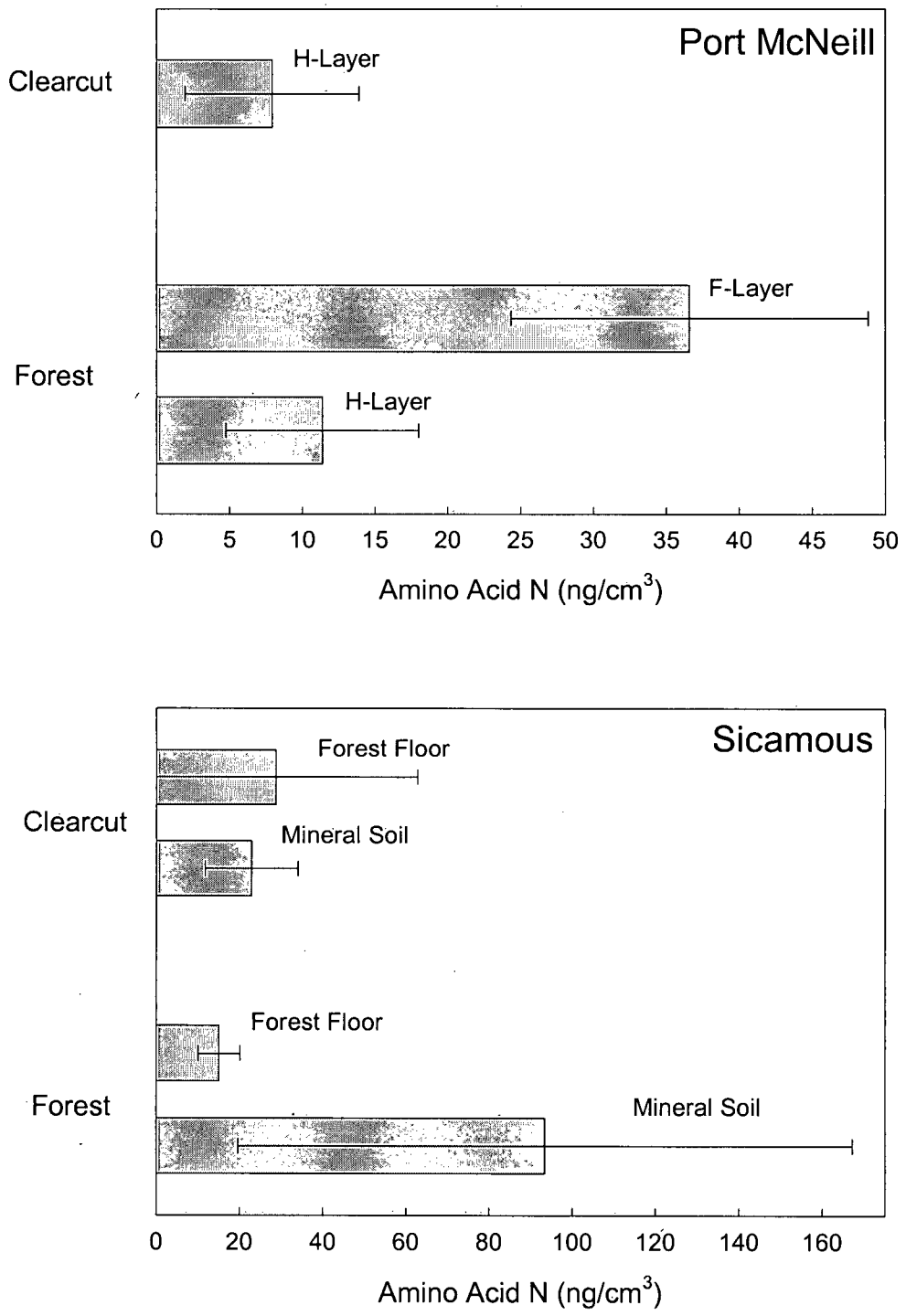

Figure 10. Concentration (ng/cm^3) of amino acid-N in each soil layer sampled from clearcuts and forests at Port McNeill and Sicamous. Each value is the mean of three blocks. Error bars indicate one standard deviation. Differences in amino acid-N concentration between soil types were not significant.

DISCUSSION

Is SON more abundant that SIN?

The finding of greater concentrations of SON than SIN in forest soil is consistent with the results of other studies (e.g., Van Cleve and White 1980; Chang et al. 1995; Huang and Schoenau 1998). The dominance of SON in forest soil probably arises from two interacting processes. First, SON accumulates because it is primarily composed of complex humic molecules that turn over slowly (Van Cleve and White 1980; Qualls and Haines 1992). Secondly, SIN is rapidly removed from the soil because plants and soil microbes can readily take it up. Together, these processes lead to higher concentrations of SON than SIN in the soil.

High ratios of SON to SIN may be characteristic of sites where plant growth is limited by N availability (Northup et al. 1995). At Port McNeill, seedling responses to N fertilization indicated that N availability was limiting growth (Weetman et al. 1993; Prescott and Brown 1998). At Sicamous, patterns of N-mineralization and nitrification were characteristic of N-poor soils (Prescott et al. in review). Thus, high ratios of SON to SIN at Port McNeill and Sicamous confirm the findings of low N availability in previous studies at the same sites.

The ratio of SON or DON to inorganic N can be reduced by inorganic N addition. Although high ratios of DON to DIN are characteristic of streamwater draining forested watersheds (e.g., Triska et al. 1984; Wissmar 1991; Hedin et al. 1995), atmospheric N deposition can cause a decline in the relative abundance of DON in streams (Mitchell, 2001; Williams et al. 2001; van Breeman 2002). Given that N fertilization causes the relative abundance of DON in the forest floor to decrease (Smolander et al. 1995; Currie et al. 1996), low DON to DIN ratios in some

European forest soils are probably also due to N deposition (e.g., Bergmann et al. 1999; Michalzik and Matzner 1999; Smolander et al. 2001). Therefore, N fertilization at Port McNeill and Sicamous would probably cause a decline in the ratio of SON to SIN in the forest soil.

Is SON content different in forests and clearcuts?

At both Port McNeill and Sicamous, forest soil SON contents tended to be higher in the forests than in the clearcuts, although differences were rarely significant. The removal of vegetation by timber harvesting can be expected to reduce concentrations of SON because aboveground litter and fine roots are important sources of SON (e.g., Qualls and Haines 1992; Huang and Schoenau 1998; Chapman et al. 2001). Five years after harvesting, the clearcuts at both sites supported only patchy growth of conifer seedlings, shrubs and herbs. In addition, forest floors in the clearcuts at both sites were more loose and friable, with fewer roots and fungal hyphae than in the forests. Thus, plant sources of SON were reduced in the clearcuts at Port McNeill and Sicamous.

The causes of the lower SON contents in the clearcuts than in the forests differed among the two sites. In the forests at Port McNeill, the top 20 cm of forest floor included both an F and an H layer. The concentration of SON in the F layer was significantly greater than the concentration of SON in the H layer. Only H-layer forest floor was present in the clearcuts at Port McNeill because the F layer had been displaced, burned off or degraded. The concentration of SON was similar in H-layer forest floor from the clearcuts and forests. This agrees with an earlier study in the same forest type, which found similar SON concentrations in H-layer forest floor from old-growth forest and 3- and 10-year old clearcuts (Chang et al. 1995). Therefore, the trend of higher SON contents in the forests at Port McNeill can be attributed to the presence of a SON-

rich F layer, which was absent in the clearcuts.

The differences in the SON content of forest soil from clearcuts and forests at Sicamous cannot be attributed to a change in the types of forest floor present. On all six sampling dates, the concentration of SON in forest floor from the clearcuts was significantly lower than that from the forest. Such a strong and consistent reduction in the concentration of SON in forest floor from clearcuts has not been documented elsewhere. The concentration of SON was higher in H-layer forest floor from 18-month-old harvested gaps than in that from European beech forest in Germany (Bauhus 1998). For up to five years after logging, SON concentrations were higher in humus from a clearcut than from an adjacent Norway spruce forest in Finland (Smolander et al. 2001). Higher concentrations of SON may occur in 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. *Quercus coccinea*, *Acer rubrum* and *Robinia pseudoacacia* logs were rich sources of dissolved organic C seven years after cutting, but the N content of solution leached from these logs was not determined (Mattson et al. 1987). Regardless of the mechanism, timber harvesting can cause increased concentrations of SON in the forest floor on some sites, but this was not found at Sicamous or Port McNeill.

At both sites, fresh litter and throughfall probably affected the concentration of SON most strongly in the upper layers of the forest soil. This is suggested in the forest at Port McNeill by the higher concentration of SON in F- than in H-layer forest floor. At Sicamous, this is suggested by the strong reduction in forest floor SON concentration in the clearcuts. Although organic N from litter and throughfall is carried downward (Qualls et al. 1991), forest-clearcut differences in the concentration of SON were not strong in the H-layer forest floor at Port

McNeill or in the mineral soil at Sicamous. Inputs of SON, which are presumably higher in the forest, are not the only factor controlling the concentration of SON in the soil because forest-clearcut differences in SON concentration were not strong in the lower soil layers.

High inputs of SON percolating from the forest floor surface into lower soil layers could be masked by the microbially-mediated production of soil organic matter. Perakis and Hedin (2001) suggested that the microbial biomass is a poor organic N sink; instead they suggested that organic N immobilized by the microbial biomass is diverted into longer-term N pools, such as plant tissue or soil organic matter. Many theories exist regarding the production of soil organic matter, but microbial biomass is widely believed to play an important role (Schnitzer and Khan 1978). In forests similar to those at Port McNeill, H-layer forest floor supported a greater microbial biomass and had higher basal respiration rates in forests than in clearcuts (Chang et al. 1995; Chang and Trofymow 1996), despite the lack of a significant difference in SON. This elevated microbial activity may have caused more rapid incorporation of SON into soil organic matter in the forests than in the clearcuts.

Differences between forests and clearcuts in the amount of SON percolating into lower soil layers could also be masked by differences in the ability of forest soil from clearcuts and forests to abiotically retain SON. In soil from the clearcuts at Sicamous, there is some evidence to suggest either increased desorption of previously bound organic N, or decreased sorption of freshly deposited SON. Water extracts of forest floor and mineral soil from the clearcuts at Sicamous contained a greater proportion of the SON extracted in KCl solution than did water extracts of soil from the forest. Extraction in salt solution removes materials sorbed by ion exchange (Qualls 2000). Thus, differences in the extractability of SON in water and in salt

solution indicate decreased retention of organic N by ion exchange in soil from clearcuts at Sicamous. Forest floor from Port McNeill did not show any difference between forests and clearcuts in the extractability of SON in water and in KCl solution.

Further evidence that timber harvesting at Sicamous may alter the retention of organic material in the forest soil was the observation that forest soil SON contents were higher in the forests than in the clearcuts but soil solution DON concentrations were higher in the clearcuts than in the forests at the same site. Based on soil solution extracted at 25 cm depth in 1994-1995, the annual flux of DON from a clearcut was more than double that from the adjacent forest (Feller 1997), and it continued to be higher in the clearcut for six years after logging (M. Feller, University of British Columbia, personal communication).

Higher DON losses and lower SON concentrations in the clearcuts at Sicamous could be caused by reduced sorption of organic material onto soil solids. Following clearcutting, hydrologic flux through the forest soil can increase (e.g., Feller et al. 2000; Qualls et al. 2000), as a result of reduced transpiration rates and greater direct inputs of precipitation to the soil surface. 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 (Feller 1997). If the pattern of greater hydrologic flux in the clearcuts is maintained for several years, the pool of organic material sorbed to soil solids may decline in the clearcuts compared to the forests.

Logging might also cause elevated DON losses and reduced SON concentrations in the clearcuts

at Sicamous by enhancing the rate of organic N desorption from soil particles. In a clearcut Douglas-fir stand in Oregon, Sollins and McCorison (1981) measured large quantities of DON in soil solution at 2 m soil depth. They suggested that clearcutting may lower the concentration of substances that inhibit decomposition of sorbed organic material, especially in the deeper soil horizons, allowing it to be metabolized and released by soil microbes. Alternatively, they proposed that the stability of sorbed organic N decreased with soil depth so that clearcutting triggered desorption of DON lower in the soil profile. However, Borchers and Perry (1992) found evidence of significant losses of sorbed organic N from the top 15 cm of mineral soil from clearcuts in south-west Oregon. Therefore, soil disturbance associated with clearcutting may trigger organic N desorption, but it is not clear if physical or biological processes are involved.

Desorption of organic N may also be caused by chemical processes. For example, ligand exchange on iron and aluminum oxides is an important means of abiotic retention of organic material (Jardine et al. 1989; Qualls 2000). Timber harvesting can decrease soil pH (e.g., Dahlgren and Driscoll 1994; Chang et al. 1995) which may trigger the release of sorbed organic N from organo-metal complexes (Jardine et al. 1989; Vance and David 1989; Dahlgren and Driscoll 1994). Following clearcutting, Dahlgren and Driscoll (1994) found that pH declined and aluminum and dissolved organic C concentrations increased in mineral soil solution from a New Hampshire spruce-fir stand. Desorption of organic N from organo-metal complexes favours the release of hydrophilic acids (Vance and David 1989), which are relatively N-rich compared to other DOC fractions (Qualls and Haines 1992; Andersson et al. 1999). Thus, changes in soil chemistry following clearcutting may cause relatively high losses of organic N from forest soil compared to losses of organic C.

What happens to SON during *in situ* incubation?

The results of the buried bag incubations indicated that changes in forest soil SON, SIN and microbial N concentrations cannot be explained simply by exchange among these three pools. During the first two incubations, the concentration of SON in forest floor at Port McNeill tended to decline more than SIN increased, while at Sicamous, the concentration of SON in forest soil tended to decline less than SIN increased. A third incubation was performed to determine if changes in SON and SIN could be explained by uptake by or input from the microbial N pool. During the third incubation, microbial N showed large increases at the same time that SON and/or SIN also increased. This indicated that a) the concentration of SON can increase or decrease during incubation and b) changes in forest soil SON concentrations cannot be directly explained by losses to or gains from the microbial N or SIN pools.

Because competition for N between soil microbes and plants can be intense, isolating the soil during incubation could free up a pool of N that would normally be taken up by plants (e.g., Jones and Hodge 1999; Schmidt et al. 1999; Vinolas et al., 2001a). According to this hypothesis, N in the microbial, SON and SIN pools would be expected to increase the most in mineral soil and/or forest floor from which plant uptake is a large N sink. H-layer material from the forest floor at Port McNeill showed similar changes in SIN, SON and microbial N in forests and clearcuts. At Sicamous, SIN, SON and microbial N showed greater increases in mineral soil from the clearcuts than from the forests. Intuitively, plant N uptake could be expected to be largest in the forests. However, a much larger fraction of N uptake may be attributed to shrubs, which are more common in the clearcuts, than to mature trees (Chapin 1983). At Sicamous, shrubs may account for up to 70% of the total N uptake from soil in the forests (M. Feller, University of British Columbia, personal communication). Therefore, it is not known whether

plant N uptake is greatest: a) in the forests, where large trees dominate but shrubs are present, or b) in the clearcuts, where shrubs and herbs dominate but vegetation cover is patchy. As a result, it is not clear whether the elimination of plant N uptake is sufficient to explain differences between forests and clearcuts in changes to microbial N, SON and SIN concentrations during incubation of soils.

Instead, N may be available from organic complexes larger than 0.45 μm, which is the generally accepted boundary between dissolved and particulate organic N (e.g., Qualls 2000; Smolander et al. 2001; Solinger et al. 2001). The predominant hypothesis is that N is not preferentially released from organic matter, but is mineralized when the C to which it is bound is oxidized (McGill and Cole, 1981; Qualls and Haines 1992). However, Carlsson et al. (1993) suggested that about 75% of the organic N in humic materials is only loosely bound and may thus be available for uptake by the microbial biomass. If this is the case, the concentration of N available from organic sources is systematically underestimated by excluding molecules > 0.45 μm.

An alternative N source could be organic N sorbed to soil particles. Nitrogen from sorbed material may not need to be desorbed in order for it to be biologically available. Qualls and Haines (1992) suggested that adsorption of organic molecules on mineral soil surfaces could concentrate this material for subsequent breakdown by soil microbes. Based on ^{13}C NMR analysis of mixed conifer forest soil in Maine, Dai et al. (1996) concluded that organic C sorbed to B horizon mineral soil particles was susceptible to microbial decomposition. Thus, estimates of readily available organic N may require inclusion of material sorbed to soil particles.

Is the abundance of SON related to moisture content and its effects on microbial activity?

The correlation analyses indicated that forest soil moisture content, SON concentration and microbial N concentration were related to each other. However, 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. This provides support for the hypothesis that SON production is higher in wet soils because of a larger microbial population (Van Cleve and White 1980; Williams 1992).

Instead of indicating that SON is produced by the microbial biomass, a positive relationship between SON and microbial N may show that the microbial biomass responds to high SON concentrations. Based on comparisons of SON extracted from forest floor using water with and without microbial inhibitors, Qualls (2000) suggested that the microbial production of SON is negligible. If microbial production of SON does not cause the positive correlation between moisture content and microbial N or SON in forest soils, physical processes may link these variables, rather than biological ones. As throughfall penetrates the forest canopy, it can become enriched in organic N collected from leaves, bark, decomposing wood and microbial tissue (Qualls et al., 2000). With greater rainfall, more SON could be carried to the forest floor, wetting the soil and elevating the concentrations of SON and microbial N independently of each other. However, this does not explain why moisture content is more strongly correlated with microbial N than with SON in the forest floor at Port McNeill.

Does SON vary among forest floor and mineral soil layers?

The two sites sampled in this study provide an opportunity to examine changes in the concentration of SON with depth in the forest floor (Port McNeill) and differences in the concentration of SON between forest floor and the mineral soil below (Sicamous). The reduction in SON concentration with depth in the forest floor, which was observed at Port McNeill, is consistent with earlier studies. Higher concentrations of SON in O_F than in O_H forest floor were reported in a European beech forest in Germany (Bauhus 1998). SON concentrations in forest floor from a boreal aspen stand declined in the order: Oi > Oe > Oa (Huang and Schoenau 1998). Concentrations of SON are higher in surface forest floors because of inputs from throughfall and fresh litter, which are rich in labile organic materials (Qualls and Haines 1992; Huang and Schoenau 1998). In addition, Qualls et al. (1991) found that the forest floor was a net sink for SIN and a net source for SON, so additional organic N is probably produced in the forest floor. Thus, the forest floor is a source of abundant SON due both to direct SON inputs in fresh litter and throughfall and to the production of additional SON.

At Sicamous, the concentration of SON in the mineral soil was about 78% of that in the forest floor. Results from previous experiments suggest that the concentration of SON in the mineral soil is between 2 and 50% of that in the forest floor (Bauhus 1998; Huang and Schoenau 1998) but reported differences between forest floor and mineral soil in these studies were probably stronger because concentrations were expressed on a mass basis. To avoid prejudicing estimates of nutrient concentrations toward higher concentrations in the forest floor, forest floor and mineral soil nutrient concentrations should be compared on a volume basis. However, even when compared on a volume basis, SON concentrations at Sicamous tended to be lower in the mineral soil than in the forest floor immediately above.

Comparisons between F- and H-layer forest floor at Port McNeill and between forest floor and mineral soil at Sicamous are consistent with findings from other studies, which suggest that the concentration of SON declines with depth in the forest soil (Bauhus 1998; Huang and Schoenau 1998). Processes that consume SON as it leaches downward include mineralisation, immobilisation and abiotic adsorption (Qualls et al. 1991). The most important of these mechanisms is probably abiotic adsorption because it occurs more rapidly than SON decomposition (Sollins and McCorison 1981; Qualls and Haines 1992; Qualls 2000). Thus, declining concentrations of SON with depth in the forest soil are caused by biotic processes of input and decomposition and by abiotic processes of adsorption and leaching.

Is amino acid-N the dominant form of SON? Does amino acid-N show the same patterns as SON?

Based on molecular fractionation of forest soil solution, free amino acids comprise only a small portion of DON (Yavitt and Fahey 1984; Qualls et al. 1991; Qualls and Haines 1991). However, few researchers have directly compared concentrations of SON and amino acid-N. In the present study, it was estimated that amino acid-N comprised only 1 to 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 to 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 relatively lower concentrations of amino acid-N in forest soil at Sicamous and Port McNeill compared to taiga forest soil.

As with SON, the amino acid-N content of these forest soils tended to be lower in the clearcuts. Because amino acid-N sources are the same as those for the larger SON pool, the same processes that cause differences in the SON content of soil from forests and clearcuts probably cause differences in amino acid-N. These include altered rates of plant input, plant and microbial uptake, physical adsorption and mineralization by exoenzymes (Kielland 1995).

At Port McNeill, the distribution of amino acid-N was similar to that for SON, with higher concentrations of amino acid-N in F-layer forest floor than in the underlying H-layer. At Sicamous, however, the average concentration of amino acid-N in the forest was higher in the mineral soil than in the forest floor above. The amino acid data were extremely variable, so this pattern may not reflect the true distribution of amino acid-N in these soils. Concentrations of amino acid-N in a *Calluna* heathland soil were much higher in the organic layer than in the underlying mineral soil (Abuarghub and Read 1988b). However, amino acid concentrations were expressed on a mass basis so these data must be interpreted with caution.

The most abundant amino acids were alanine, threonine, arginine, proline, serine glycine and glutamine, though the relative quantities of these amino acids tended to change by site and by treatment. With the exception of proline, these amino acids have been among the most abundant found in soil extracts from other studies (e.g., Kielland 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 is the only amino acid to show a pattern that may be related to differences between soil types or between forests and clearcuts. High concentrations of arginine were associated with F-layer forest floor at Port McNeill. At Sicamous, high concentrations were found in forest floor from the forests and the clearcuts and in mineral soil from forests. Because arginine functions in root N storage (Van den Driessche and Webber 1977; Lipson et al. 1996), elevated levels of arginine could be a result of soil sample contamination by damaged fine roots. However, at Sicamous, the density of fine roots was much lower in forest floor from the clearcuts than from the forests, yet arginine levels were abundant in forest floor from both treatments. In other studies, where concentrations of amino acids in soil extracts and plant roots were compared, no evidence was found for contamination of soil samples by amino acids from root tissue (Ivarson and Sowden; 1969; Kielland 1995). Thus, contamination of forest soil samples by damaged fine roots does not adequately explain the distribution of arginine in these soils.

CONCLUSIONS

Is SON more abundant than SIN?

In all soil types examined, the concentration of SON was significantly greater than that of SIN. This was attributed to the slow turnover of SON and the rapid uptake of SIN by plants and soil microbes, which would result in a greater accumulation of SON relative to SIN.

Is SON content different in forest and clearcuts?

SON content tended to be lower in the clearcuts than in the forest but treatment effects had different causes at the two sites. At Port McNeill, higher SON contents in the forests were due to the presence of a SON-rich F layer, which was absent in the clearcuts. At Sicamous, where the forest floor was much thinner, differences in SON content between forests and clearcuts were due to significantly lower concentrations of SON in the forest floor from the clearcuts.

These observations suggest that litter inputs from the forest canopy are an important source of SON. Other studies have shown that organic N from litter percolates into the lower soil layers. However, treatment differences were not strong in H-layer forest floor at Port McNeill or in mineral soil at Sicamous. Higher inputs of SON to soils in the forest may be masked by more rapid incorporation into the soil organic matter or by more effective adsorption on forest floor and mineral soil particles.

Clearcutting can affect the rate of adsorption to or desorption from the forest floor or mineral soil by numerous mechanisms. In other studies, more rapid hydrologic flux through forest soils or changes in soil chemical conditions, such as pH, have been shown to affect the amount of

organic material leached from the soil. At Sicamous, treatment differences in the relative abilities of water or salt solution to remove SON from forest floor and mineral soil suggest that SON is retained less effectively in the clearcuts. This may explain why treatment differences in SON were the opposite of those for DON, which was higher in soil solution from a clearcut than from a forest at Sicamous.

What happens to SON during *in situ* incubation?

During one-month buried bag incubations, changes in the concentrations of SIN, SON and microbial N were not sufficiently explained by interchange among these three N pools. Instead, there appeared to be one or more alternative sources and sinks for SON. Because SON is defined by its size rather than by its chemical structure, some organic N may be excluded which is actually available for microbial uptake. Organic N sorbed to soil particles may also be accessible to the microbial biomass.

Is the abundance of SON related to moisture content and its effects on microbial activity?

At both sites, moisture content was positively correlated with both SON and microbial N. This might suggest that wet forest soils support a larger microbial population, which in turn produces a greater quantity of SON. Such a relationship may be especially important at Sicamous, where SON and microbial N were also positively correlated. A positive correlation between moisture content and SON or microbial N could be caused by other processes, e.g. SON-enriched throughfall and it effects on the size of the microbial community.

Does SON vary among forest floor and mineral soil layers?

At both sites, the concentration of SON tended to decline with depth. This pattern is probably

caused by high SON inputs from throughfall and litter at the forest floor surface.

Is amino acid-N the dominant form of SON? Does amino acid-N show the same patterns as SON?

Amino acid-N formed approximately 1 to 1.5% of the SON. Although this suggests that amino acid-N is not abundant in these forest soils, low concentrations of amino acid-N could be a result of either low production rates or high consumption rates.

At both sites, amino acid-N showed a similar treatment effect to SON, with higher concentrations in the forests than in the clearcuts. At Port McNeill, amino acid-N was much higher in the F- than in the H-layer forest floor, which is similar to the pattern for SON. In the forests at Sicamous, however, average amino acid-N concentrations were higher in the mineral soil than in the forest floor. The reason for this is not known.

As has been found in other studies, neutral amino acids were the most abundant, probably because they readily diffuse in soil solution. At both sites, arginine, which is a basic amino acid, showed a trend toward higher concentrations in soils from the forest than from the clearcut. Elevated concentrations of arginine, which functions in root N storage, are probably not due to fine root damage because high arginine levels were found in forest floor from the clearcuts, where fine roots were noticeably less abundant.

These findings illustrate our poor understanding of the sources and sinks for SON. Most SON is probably not immediately available for uptake by plants or soil microbes. However, timber harvesting appears to affect the ability of forest soils to sorb this material and prevent its loss to

leaching. Although the relationship between SON and the microbial biomass is not clear, soil microbes may be able to access some of this sorbed organic N. If the ability to retain SON is reduced in some forest soils, this may affect the pool of available N in the future.

Future Research

Amino acid-N, which forms only a small fraction of the SON in these soils, is extremely labile. Most of the SON in forest soil is more recalcitrant. Thus, high concentrations of SON do not necessarily indicate greater N availability. Findings from this study suggest that abiotic processes of SON production and consumption are important in controlling the concentration of SON in these soils, and that some of this sorbed organic N may be available to soil microbes. Further work is needed to monitor the effects of timber harvesting on the chemical nature of SON (e.g. hydrophobicity, acidity, molecular size) and its ability to decompose. This information will help determine the relative importance of biotic and abiotic processes of SON immobilisation.

Correlation analyses suggest that forest soil moisture content and the concentrations of SON and microbial N are somehow related. However, it is unclear whether the positive correlation between moisture content and SON, for example, indicates a causative relationship. Laboratory incubations of these soils, where moisture and litter inputs are manipulated, might shed some light on the interactions between SON and microbial N.

To explain potential differences in the effects of timber harvesting on SON and DON, the ability of the forest floor and mineral soil to sorb organic N should be further examined. It must be

determined whether logging can trigger desorption of organic N from these soils. The most important mechanisms for organic N sorption in these soils must also be identified. This knowledge will help foresters predict the impact of management decisions on potential leaching losses of organic N from soils. It also may help explain the similar concentrations of SON in H-layer forest floor from the clearcuts and forests at Port McNeill, and indicate whether the clearcuts at Sicamous are losing greater proportions of their SON from the soil.

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