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Transferring soils from high- to low-elevation forests increases nitrogen cycling rates: climate change implications

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Abstract

We assessed the potential impact of global warming resulting from a doubling of preindustrial atmospheric CO_2 on soil net N transformations by transferring intact soil cores (0–15 cm) from a high-elevation old-growth forest to a forest about 800 m lower in elevation in the central Oregon Cascade Mountains, USA. The lower elevation site had mean annual air and soil (10-cm mineral soil depth) temperatures about 2.4 and 3.9 °C higher than the high-elevation site, respectively. Annual rates of soil net N mineralization and nitrification more than doubled in soil transferred to the low-elevation site (17.2–36.0 kg N ha^{-1} and 5.0–10.7 kg NO_3^-–N ha^{-1}, respectively). Leaching of inorganic N from the surface soil (in the absence of plant uptake) also increased. The reciprocal treatment (transferring soil cores from the low- to the high-elevation site) resulted in decreases of about 70, 80, and 65% in annual rates of net N mineralization, nitrification, and inorganic N leaching, respectively. Laboratory incubations of soils under conditions of similar temperature and soil water potential suggest that the quality of soil organic matter is higher at the high-elevation site. Similar *in situ* rates of soil net N transformations between the two sites occurred because the lower temperature counteracts the effects of greater substrate quantity and quality at the high elevation site. Our results support the hypothesis that high-elevation, old-growth forest soils in the central Cascades have higher C and N storage than their low-elevation analogues primarily because low temperatures limit net C and N mineralization rates at higher elevations.

Keywords: coniferous forest, global warming, nitrification, nitrogen loss, nitrogen mineralization, Oregon

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Introduction

Over the next 50–100 years, anthropogenically induced climate warming from the production of greenhouse gases is hypothesized to increase global mean annual temperature by 2–5 °C (Hansen *et al.* 1981; Houghton *et al.* 1992). Because most biological and chemical processes that occur within ecosystems are temperature dependent, global warming will undoubtedly directly alter ecosystem function. However, ecosystem-level responses to global warming can not be predicted from simple direct responses of ecosystem components, because of the vast network of feedbacks that exist within terrestrial ecosystems. Indeed, feedbacks between the biosphere and the atmosphere may result in the dampening or magnification of climate change (Perry *et al.* 1991).

The manner by which increases in soil temperature influence soil nitrogen (N) cycling may be key in determining how terrestrial ecosystems respond to global warming. This is because N frequently limits the net primary productivity of terrestrial ecosystems (Binkley & Hart 1989; Vitousek & Howarth 1991), and soil N transformations have been shown to be fairly responsive to changes in temperature (Focht & Verstraete 1977; Malhi *et al.* 1990; Binkley *et al.* 1994; Stark & Firestone 1996). Increased N availability in soil resulting from warmer

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temperatures may result in greater net ecosystem production, increasing net carbon (C) sequestration in terrestrial ecosystems, and thus dampening the contribution of CO_2 to global warming. Hence, changes in the amount of available N are likely to strongly influence the ability of terrestrial ecosystems to take up and store more CO_2-C, the greenhouse gas most responsible for global climate change (Perry *et al.* 1991).

Many different experimental approaches have been used to study the potential impacts of climate change on terrestrial ecosystems, including controlled-climate laboratory studies (Billings *et al.* 1983), and experimental field manipulations using plastic enclosures (Shaver *et al.* 1986), buried heating cables (Van Cleve *et al.* 1990; Peterjohn *et al.* 1994), and infrared radiators (Harte *et al.* 1995). Natural temperature gradients caused by changes in altitude (Graham *et al.* 1990; Perry *et al.* 1991: Jonasson *et al.* 1993) or aspect (Joslin & Wolfe 1993) also have been used as surrogate experimental systems of climate change. All of these experimental approaches have distinct advantages and disadvantages, with infrared radiators producing the most realistic effects (Harte *et al.* 1995). However, the expense of most direct manipulative approaches limits the extent to which these methods can be applied across the wide array of terrestrial ecosystems. Combining different approaches, such as the use of natural temperature gradients coupled with direct manipulation (soil or plant–soil reciprocal transplants), may provide a powerful and cost-effective tool for assessing the potential impact of climate change on terrestrial ecosystems.

The objectives of the research described here were to assess the effects of transferring soil between high- and low old-growth forests on rates of net N mineralization, net nitrification, and inorganic-N leaching from the surface mineral in the absence of plant uptake. We then interpreted the results from this experimental design in the context of the potential impacts of global climate change over the next half-century on soil N transformations in these forests. We chose old-growth coniferous forests of the US Pacific Northwest as an ecosystem-type to conduct this study because large differences in C and N stores exist between high- and low-elevation forests in this region, and these differences have been hypothesized to be temperature-driven (Perry *et al.* 1991).

Materials and methods

Study sites

Our study sites consisted of two old-growth forest stands (dominant trees > 450 y old) that differed in mean daily air temperature by 2.4 °C, primarily due to an altitudinal difference of about 820 m (Table 1). The corresponding difference in mean annual soil temperature (10-cm mineral soil depth) was 3.9 °C. Seasonal differences between the sites in air and soil temperatures were similar in magnitude to these annual differences. The old-growth forests were located within the HJ Andrews Experimental Forest, in the central Oregon Cascades (44°14′N, 122°11′ W). The climate in this region is quasi-Mediterranean, with mild, wet winters and warm, dry summers.

The low-elevation site was located near Reference Stand 2 at an elevation of 490 m, and received ≈ 1880 mm of precipitation during the one-year study period. This stand is composed primarily of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees, with western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and scattered western redcedar (*Thuja plicata* Donn ex D. Don) trees accounting for the rest of the stand. The stand is on a 35% west-facing slope, and the soil is an unclassified fine-loamy, mixed, frigid Typic Dystrochrept.

The high-elevation site was located near Frissell Ridge at an elevation of 1310 m (Table 1). Approximately 1890 mm of precipitation fell upon this stand during the one-year study period. This stand is dominated by Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) and Douglas-fir, and is on a 50% slope with a south-westerly aspect. The soil is an unclassified loamy-skeletal, mixed, frigid Typic Haplumbrept. Both stands have moderately thick (averaging about 10 cm), mor-type forest floors

Table 1 Selected site characteristics of high- and low-elevation old-growth forests in the central Oregon Cascades

Site	Elevation (m)	Precipitation[1] (mm)	T_a[1] (°C)	T_s[1] (°C)	pH (1:2 w/w Soil:H_2O)[2]	Total C[2] (g kg^{-1})	Total C[2] (kg ha^{-1})	Total N[2] (g kg^{-1})	Total N[2] (kg ha^{-1})
High	1310	1890	5.9	4.9	5.49 (0.09)	141(20)	74.7 (11.2)	5.65 (0.35)	3000 (238)
Low	490	1880	8.3	8.8	5.73 (0.09)	54.4 (6.2)	43.7 (5.16)	2.27 (0.17)	1830 (148)

[1]Annual precipitation and mean annual air (T_a) and soil (T_s) (10-cm mineral soil depth) temperatures measured during the field study at meteorological stations located near each site.
[2]Values shown are means (and standard errors) for each mineral soil property (0–15 cm); $n = 8$ for all properties except for total C at the high-elevation site where $n = 10$.

with moderately acidic surface mineral soils (Table 1). The high-elevation stand has substantially greater total C and N concentrations (g kg^{-1}) and contents (kg ha^{-1}) within the surface mineral soil (Table 1).

Experimental design, soil sampling procedures, and field incubations

Within each stand, eight 3 × 3 m plots were established systematically along a 70-m transect perpendicular to the slope. The starting points of the transects were chosen at random. Soil sampling locations within each plot also were determined at random. On each of two sampling dates (18–19 October 1990 and 4–5 June 1991) and after carefully peeling back the forest floor (O horizon), three adjacent intact soil cores (0–15 cm) were removed using 5-cm inner diameter × 20-cm long, thin-walled polyvinyl chloride (PVC) pipe that had been sharpened at one end. One of these cores (the initial core) was placed in a polyethylene bag, kept cool (≈ 4 °C), and returned to the laboratory for analysis (within 72 h of sampling). These soil samples were used for laboratory incubations and determinations of initial inorganic-N pool sizes, gravimetric water content, and microbial biomass (see below). The other two cores were used to assess net N mineralization and net nitrification rates under field conditions using the resin-core method (Di Stefano & Gholz 1986; Binkley & Hart 1989).

Resin cores consisted of intact soil cores capped at both ends by ion exchange resin (IER) bags. The purpose of the top IER bag is to capture incoming ions originating from above the soil core (i.e. forest floor), while allowing water to enter freely. The purpose of the bottom IER bag is to capture ions leached from the mineral soil contained within the core, while allowing water to exit. The IER bags were constructed by placing 30 mL (7.8 g oven-dry equivalent) of cation + anion exchange resin beads (JT Baker #M-614 16–50 mesh mixed-bed IER that had been pre-extracted with 2 M KCl; Hart & Binkley 1984) in nylon stockings that contained a 5-cm diameter latex rubber tubing ring, and then were tied shut. The resulting bag fit tightly within the PVC pipe. However, to insure against soil solution losses through boundary flow along the inner PVC wall, silicon glue was used to seal the outside ring to the PVC tube. One of the two resin cores was returned to its original hole within the plot (*in situ* core), while the second paired resin core was transferred to the other old-growth forest site for incubation (transferred core). After making sure that a solid contact was made between the bottom IER bag and the underlying soil, the overlying organic horizon was then carefully replaced over the soil. Soil cores sampled in October 1990 were incubated until the June 1991 sampling (hereafter called the 'winter incubation'). Soil cores sampled in June 1991 were incubated until 21–22 October 1991 (hereafter called the 'summer incubation'). This experimental design resulted in 8 replicates per soil type, treatment (incubated *in situ* or transferred), and incubation period (winter and summer).

After the incubation period, resin cores were removed and kept cool until they were returned to the laboratory and processed (within 72 h). Ion exchange resin bags were removed from the resin cores, air-dried, and resin beads extracted with 100 mL of 2 M KCl. Ammonium and NO_3^- contents collected on the IER were adjusted for incomplete recoveries using a single 2 M KCl extraction (Hart & Binkley 1984) determined from a separate experiment (80 and 74% extraction efficiencies for NH_4^+ and NO_3^-, respectively; data not shown). We estimated the leaching flux of inorganic N from the surface mineral soil in the absence of plant uptake by dividing the amount of inorganic N accumulated on the IER bags below the soil core by the surface area of the IER bag (≈21.2 cm^2). Net N mineralization was calculated by adding this amount to the difference in soil inorganic pools (expressed on an areal basis using the mean bulk density of each initial-incubated soil core pair) measured before and after incubation. Similarly, net nitrification was calculated by adding the quantity of NO_3^- accumulated on the bottom IER bag to the net change in the soil core NO_3^- pools.

Laboratory incubations and analyses

Soils from initial and incubated soil cores were sieved field-moist through a 4-mm mesh screen. Soil water contents were not altered from their field values prior to laboratory incubation because all soils had water contents near field capacity (≈ – 33 kPa soil water potential) at the time of sampling, and soil water contents varied little among plots within a site. From each initial soil sample on both sampling dates, two subsamples (≈ 10-g field-moist mass) were weighed into 20-mL scintillation vials. One was incubated for 30 days at 22 ± 1 °C (aerobic incubation subsample); the other subsample was fumigated with ethanol-free chloroform vapour for 24 h and then incubated for 10 days at 22 ± 1 °C after removing the chloroform vapour with repeated evacuations (chloroform fumigation-incubation subsample). Two additional subsamples (≈ 15-g field-moist mass) were placed in 120-mL specimen containers. To one of these specimen containers, 50 mL of deionized water were added making sure all the soil material was completely wetted (anaerobic incubation). These subsamples were then incubated at 40 ± 1 °C for 7 days. After 7 days, the subsamples were extracted with 50 mL of 4 M KCl. The other subsample in the specimen container was immediately extracted with 100 mL of 2 M KCl and served as the initial inorganic-N pool size estimate for

field and laboratory incubations. Anaerobically mineralizable N was calculated by subtracting the initial NH_4^+ pool size from the post-incubation NH_4^+ pool size (Binkley & Hart 1989).

Vials containing soils used for aerobic and chloroform-fumigation incubations were placed within 0.975-L Mason jars and sealed with air-tight lids fitted with a butyl rubber septum. About 30 mL of deionized water were placed in a 120-mL specimen container within each Mason jar to maintain soil wetness (Hart *et al.* 1994).

Carbon dioxide concentrations were determined initially and after each 10-day period in the headspace of Mason jars containing the aerobic incubation (October 1990 sampling date only) and chloroform-fumigation incubation subsamples by sampling the headspace gas with a 1-mL syringe. The headspace of each Mason jar was mixed repeatedly using a 60-mL syringe prior to taking gas samples. Headspace gas samples were introduced into a Carle AGC Series 100 isothermal gas chromatograph fitted with a thermal conductivity detector (EG & G Chandler Engineering, Broken Arrow, OK, USA). For the 30-day aerobic incubation subsamples, Mason jars were flushed with ambient air (≈360 μmol CO_2/mol air) following each CO_2 measurement (Hart *et al.* 1994). Carbon dioxide evolution during the 30-day aerobic incubation (microbial respiration) was calculated from the summation of increases in headspace CO_2 concentrations (above ambient air) during each 10-day incubation period.

After both incubations, aerobic and chloroform-fumigation incubation subsamples were extracted with 75 mL of 2 M KCl. Net N mineralization rates were calculated for each subsample by subtracting initial inorganic-N pool sizes from inorganic-N pool sizes determined after 30 days of aerobic incubation. Net nitrification rates were calculated by subtracting initial NO_3^- pool sizes from post-incubation NO_3^- pool sizes (Binkley & Hart 1989).

Microbial biomass C was calculated by dividing the CO_2-C evolved from the chloroform-fumigation incubation subsample (C_F) by 0.41 (Voroney & Paul 1984). Microbial biomass N was calculated by dividing the net accumulation of NH_4^+–N during the fumigation-incubation (N_F) by a value k_N, determined using the equation (Paul & Clark 1989): $k_N = 0.8 \times (C_F/N_F)^{-0.43}$.

All KCl-soil and KCl-resin suspensions were shaken for 1 h on a mechanical shaker and then filtered through Whatman no. 40 filter paper. The filter papers were pre-leached with 50 mL of 2 M KCl to remove any NH_4^+ and NO_3^- initially present. Ammonium (salicylate/nitroprusside; Keeney & Nelson 1982) and NO_3^- (diazotization following cadmium reduction; Keeney & Nelson 1982) were determined using an Alpkem RFA 300 Rapid Flow Analyser (Clackamas, OR, USA). Soil total C concentrations at the high-elevation site were determined from a previous study (DA Perry, *unpublished data* 1987), while soil total C concentrations at the low-elevation site were determined on the initial soil samples taken in October 1990. All total C analyses were conducted on a LECO 12 C analyser (LECO Corp., St. Joseph, MI, USA). Soil total N concentrations for both sites were determined on the initial soil samples taken in October 1990 using micro-Kjeldahl digestion (Bremner & Mulvaney 1982) followed by NH_4^+ analysis. Gravimetric soil water contents of each sieved soil was determined from a separate subsample (≈ 15–20 g) oven-dried at 105 °C for 48 h. Field and laboratory estimates of labile N pools and net N transformation rates were expressed both on a per unit oven-dry soil mass (or area in the case of field rates) and a per unit mass of soil total N basis. Values expressed on a per unit mass of soil total N basis were used to examine potential differences in soil substrate quality between the two stands (*sensu* Powers 1990), given that they differed considerably in soil total N concentration (Table 1).

Statistical analyses

We used paired *t*-tests to assess treatment effects (*in situ* or transferred soil incubation) on soil properties and processes for a given forest site and sampling date or incubation period. Because some of the variables exhibited non-normality, we also subjected the paired data to the nonparametric Wilcoxon signed rank test. All statistical analyses were performed using SigmaStat V. 2 software (Jandel Scientific, San Rafael, CA, USA) at the $P = 0.05$ significance level (unless otherwise noted).

Results

Effects of soil transfer on in-field rates of soil net N transformations and leaching

Soil transfer from the high- to low-elevation site resulted in a more than doubling in the annual rates of net N mineralization (Fig. 1) and net nitrification (Fig. 2). Conversely, transferring soils from the low- to high-elevation site resulted in about a 70% reduction in the annual net N mineralization rate (Fig. 1), and about an 80% reduction in the annual rate of net nitrification (Fig. 2). Furthermore, the effects of soil transfer on net N mineralization and net nitrification for each soil were similar for both incubation periods (Table 2).

Annual leaching of inorganic N from surface soils in the absence of plant uptake was significantly higher ($P < 0.10$; paired *t*-test and Wilcoxon signed rank test) in soils transferred from the high-elevation to the low-elevation site (Fig. 3), but this increase was only about 30%. In contrast, annual leaching of inorganic N from the surface

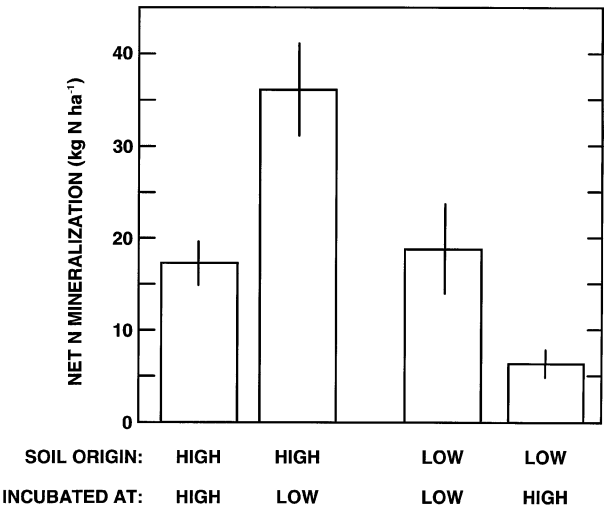

Fig. 1 The effect of transferring soils between high- and low-elevation old-growth coniferous forests on annual rates of net N mineralization. Intact mineral soil cores (0–15 cm) from a high-elevation (1310 m) and a low-elevation (490 m) old-growth conifer site were either incubated in the site of origin (*in situ*) or transferred and incubated in the other site. Vertical bars denote ± 1 SE of the mean (n = 8). Transferred soils had significantly different annual rates of net N mineralization compared to the same soils incubated *in situ* ($P < 0.05$; paired t-test and Wilcoxon signed rank test).

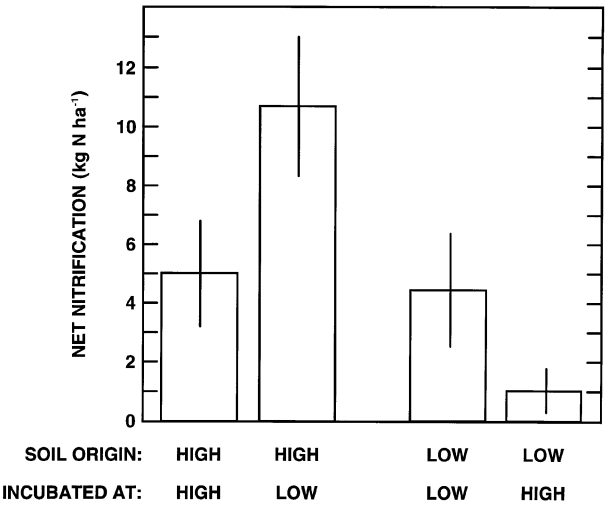

Fig. 2 The effect of transferring soils between high- and low-elevation old-growth coniferous forests on annual rates of net nitrification. Intact mineral soil cores (0–15 cm) from a high-elevation (1310 m) and a low-elevation (490 m) old-growth conifer site were either incubated in the site of origin (*in situ*) or transferred and incubated in the other site. Vertical bars denote ± one standard error of the mean (n = 8). Transferred soils had significantly different annual rates of net nitrification compared to the same soils incubated *in situ* ($P < 0.05$; paired t-test and Wilcoxon signed rank test).

soil was reduced by about 65% when soils from the low-elevation site were transferred to the high-elevation site (Fig. 3). In most cases, more NH_4^+ was leached than NO_3^- (Table 2). High- and low-elevation soils incubated *in situ* had similar annual rates of net N mineralization, net nitrification, and N leaching (Figs 1–3).

Net N mineralization and net nitrification rates were generally greater over the summer incubation period (≈5 months; mean daily soil temperatures of 9.2 and 13.6 °C for the high- and low-elevation sites, respectively) than during the winter incubation period (≈7 months; mean daily soil temperatures of 2.2 and 5.8 °C for the high- and low-elevation sites, respectively) (Table 2). In contrast, leaching of inorganic N from surface soils was generally greater during the winter than the summer period, with the exception of the high-elevation soil incubated at the high-elevation site (Table 2). During both incubation periods, incubation location did not significantly effect the water content of the soil contained within the resin core at the end of the incubation period ($P > 0.10$; Paired t-test and Wilcoxon signed rank test; data not shown).

When incubated at the same site, soil from the high-elevation site generally had higher rates of net N transformations than soil from the low-elevation site, regardless of whether the rates were expressed per unit area or per unit mass of soil total N (Table 2). However, the differences between soils were smaller when the rates were expressed per unit mass of total N.

There were few statistically significant effects of soil transfer on inorganic-N leaching rates when analysed by incubation period (Table 2). During the winter, NO_3^- leaching was significantly higher in high-elevation soils transferred to the low-elevation site, and NO_3^- leaching was significantly lower in soils transferred from the low- to the high-elevation site. No other significant differences were found in inorganic N leaching resulting from soil transfer between sites.

Comparison of the quality of mineral soils from high and low-elevation old-growth forest sites

Surface mineral soil from the high-elevation site had significantly higher mean water contents, extractable NH_4^+ pool sizes, and microbial biomass C and N than soil from the low-elevation site on both sampling dates, when values were expressed on a per mass of soil basis (Table 3). Extractable soil NO_3^- concentrations in soils from both sites and on both sampling dates were all < 0.01 mg N kg^{-1}. When microbial biomass N-values were expressed per unit mass of soil total N, however, the low-elevation soil had higher mean values on both sampling dates. Microbial C per unit soil total C-values were not calculated and analysed statistically because

Table 2 Mean values (and standard errors) of net nitrogen mineralization, net nitrification, and inorganic N leaching in high- and low-elevation, old-growth forest mineral soil cores (0–15 cm) incubated at both sites[1]

Incubation Period	Soil	Site	Net N Mineralization (kg N ha^{-1})	Net N Mineralization (g N $kg\ N^{-1}$)	Net Nitrification (kg N ha^{-1})	Net Nitrification (g N $kg\ N^{-1}$)	Leaching[2](kg N ha^{-1}) NH_4^+	Leaching[2](kg N ha^{-1}) NO_3^-	Leaching[2](kg N ha^{-1}) $NH_4^+ + NO_3^-$
Winter	High	High	3.29a	1.24a	0.49a	0.19a	1.07a	0.44a	1.51a
			(1.31)	(0.50)	(0.37)	(0.14)	(0.18)	(0.32)	(0.49)
		Low	7.48b	3.36b	2.76b	1.24b	0.95a	2.14b	3.09a
			(2.99)	(1.48)	(1.86)	(0.86)	(0.20)	(1.60)	(1.75)
	Low	High	1.28a	0.68a	0.23a	0.12a	0.60a	0.20a	0.80a
			(0.71)	(0.36)	(0.21)	(0.11)	(0.12)	(0.18)	(0.26)
		Low	7.14b	5.06b	2.41b	1.83b	0.95a	1.54b	2.49a
			(3.62)	(3.02)	(1.84)	(1.52)	(0.41)	(1.31)	(1.72)
Summer	High	High	13.9a	5.59a	4.53a	1.91a	1.73a	0.62a	2.35a
			(2.0)	(0.85)	(1.77)	(0.81)	(0.39)	(0.32)	(0.62)
		Low	28.5b	10.8b	7.94b	3.06b	1.47a	0.51a	1.98a
			(4.0)	(1.98)	(2.21)	(0.96)	(0.17)	(0.15)	(0.17)
	Low	High	4.94a	2.57a	0.80a	0.44a	0.47a	0.03a	0.51a
			(1.34)	(0.68)	(0.75)	(0.42)	(0.11)	(0.02)	(0.11)
		Low	11.6b	6.12b	2.05a	1.19a	0.82a	0.16a	0.98a
			(3.2)	(1.77)	(1.50)	(0.84)	(0.22)	(0.09)	(0.31)

[1]Mean values followed by different letters denote significant differences ($P < 0.05$; paired *t*-test and Wilcoxon signed rank test) between sites within a given soil and incubation period.
[2]Determined from the amount of N adsorbed on ion exchange resin bags placed below incubated mineral soil cores.

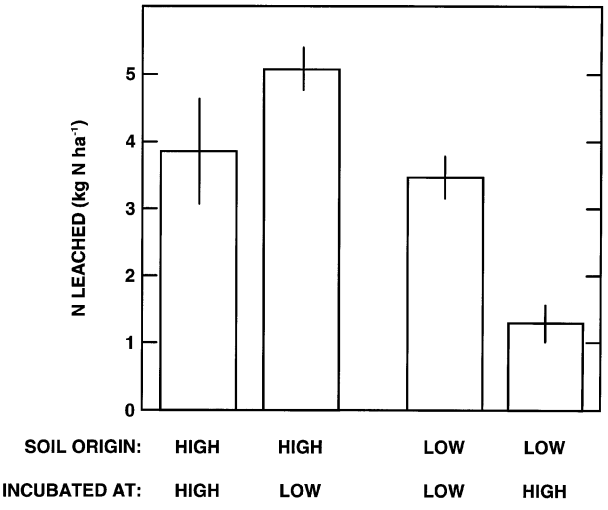

Fig. 3 The effect of transferring soils between high- and low-elevation old-growth coniferous forests on annual rates of inorganic N leaching from surface soils. Intact mineral soil cores (0–15 cm) from a high-elevation (1310 m) and a low-elevation (490 m) old-growth conifer site were either incubated in the site of origin (*in situ*) or transferred and incubated in the other site. Inorganic-N leaching rates were determined in the absence of plant uptake from the amount of inorganic N collected on ion exchange resins placed at the bottom of soil cores. Vertical bars denote ± one standard error of the mean ($n = 8$). Transferred soils had significantly different annual rates of inorganic N leaching compared to the same soils incubated *in situ* ($P < 0.10$ and 0.05 for high- and low-elevation soils, respectively; paired *t*-test and Wilcoxon signed rank test).

total soil C-values for the high-elevation site were not measured on the same soil subsamples as microbial C (see above); however, the low-elevation soil also appears to support more microbial C per soil total C as well (about 13 and 21 g microbial-C kg^{-1} total-C for high- and low-elevation soils, respectively; data not shown).

Mean values of anaerobically mineralizable N and net mineralization of C (i.e. microbial respiration) and N during aerobic laboratory incubations, when expressed on a per unit soil mass basis, also were significantly higher in soil from the high-elevation compared to the low-elevation soil on both sampling dates (Table 3). However, differences in these values between the two soils were mixed when the soil N availability values were expressed per unit mass of soil total N (Table 3). For instance, net N mineralization and nitrification rates per unit total N were significantly higher in the high-elevation soil in June 1991 but not in October 1990; low-elevation soils had significantly higher AMN values per unit soil total N in October 1990 but not in June 1991 (Table 3).

Discussion

Effect of elevation on soil net N transformations

We found that net N mineralization and nitrification rates in the two forest soils incubated *in situ* were similar when expressed on an areal basis. This similarity in soil net N transformation rates appears to be due to differ-

Table 3 Mean values (and standard errors) of soil water content, extractable ammonium and microbial biomass carbon and nitrogen pool sizes, and laboratory estimates of available carbon and nitrogen in old-growth forest mineral soils (0–15 cm) from high and low elevation sites[1]

Sampling date	Soil	Soil Water Content (kg kg^{-1})	Microbial				Aerobic Net N Mineralization	Net Nitrification	Anaerobically Mineralizable N
			[2]Extractable $NH_4^+ - N$ (mg kg^{-1})	C (g C kg^{-1})	N (mg N kg^{-1})	Respiration (g N kg N^{-1})(g C kg^{-1})	(mg N kg^{-1}) (g N kg N^{-1})	(mg N kg^{-1}) (g N kg N^{-1})	(mg N kg^{-1}) (g N kg N^{-1})
October 1990	High	0.643b (0.052)	1.13b (0.10)	1.69b (0.15)	250b (34)	43.1a (3.1)	1.40b (0.19)	8.35b 1.42a (2.49) (0.35)	4.94b 0.83a (1.50) (0.20)	63.2b 10.9a (9.1) (0.9)
	Low	0.374a (0.019)	0.85a (0.08)	1.09a (0.17)	153a (19)	65.8b (5.0)	0.77a (0.18)	3.63a 1.62a (0.77) (0.36)	1.74a 0.80a (0.05) (0.06)	34.7a 14.7b (5.8) (1.5)
June 1991	High	0.754b (0.022)	1.99b (0.27)	1.88b (0.17)	265b (18)	48.6a (5.9)	nd[3]	17.2b 3.30b (3.6) (0.78)	4.46b 0.79b (2.93) (0.52)	60.6b 11.1a (3.2) (0.9)
	Low	0.443a (0.015)	0.85a (0.15)	1.20a (0.21)	173a (30)	77.1b (13.0)	nd	1.20a 0.54a (0.5) (0.25)	− 0.34a − 0.15a (0.01) (0.01)	28.9a 12.9a (5.9) (2.6)

[1]Mean values followed by different letters denote significant differences ($P < 0.05$; paired *t*-test and Wilcoxon signed rank test) between soils within a given sampling date.
[2]Mean extractable NO_3^--N concentrations were all < 0.01 mg kg^{-1}.
[3]Not determined.

ences in substrate quality and quantity coupled with soil temperature differences between the two sites. For instance, the high-elevation soil has a higher substrate quality, as indicated by the higher net rates of N mineralization and nitrification per unit mass of soil total N under controlled laboratory conditions (Table 3). The high-elevation soil also has greater soil total N (Table 1), which enhanced the differences in soil net N transformations when expressed on a per unit soil mass of soil basis (Table 2). However, greater temperature limitation of these processes under field conditions at the high-elevation site results in similar annual *in situ* rates within the two forests (Figs 1 and 2).

Morecroft *et al.* (1992) also found little change in soil net N mineralization and nitrification rates measured *in situ* during the growing season along two altitudinal transects in the Scottish Highlands. However, soil total N concentration did not vary systematically with elevation at their sites. They concluded that comparable rates of soil net N transformations in high- and low-elevation sites occurred despite lower temperatures at higher elevations because of greater availability of labile N compounds at higher elevations. They suggested that larger labile N-pools resulted from lower soil temperatures over winter at the high-elevation sites, and that if rates would have been measured over the entire year, the high-elevation sites would have had lower values.

Marrs *et al.* (1988) found that soil net N transformations decreased with altitude in tropical rain forests in Costa Rica, but laboratory incubations suggested that temperature was not the limiting factor. Their results indicated that reduced rates of these processes occurred at higher elevations because of the high water content of the montane soils.

Powers (1990) found the highest rates of soil net N transformations at intermediate elevations along altitudinal gradients in northern California, USA. His results suggested that soil water availability limited soil net N transformations at the low-elevation sites, while low soil temperatures limited these processes at the higher elevations.

It is clear from these studies of soil net N transformations along altitudinal gradients that only with reciprocal transplant of soils coupled with laboratory incubations is it possible to clearly isolate the factors controlling these processes under field conditions. Furthermore, these studies illustrate that all four factors (i.e. substrate quality and quantity, temperature, and water content) interact in regulating soil net N transformations, and these interactive effects must be considered in any realistic model of the potential effects of climate change on soils.

Effects of soil transfer on net N transformations

The dramatic increases in net N mineralization, net nitrification, and (to a lesser degree) inorganic N leaching resulting from transferring soils from the high- to the low-elevation site clearly indicate that soil N cycling processes in these old-growth coniferous forests are controlled substantially by temperature. We attribute these changes in net transformation rates entirely to changes in soil temperature for the following reasons: the same soil was incubated at each site eliminating any potential effect of differences in substrate quality on net N transformations; and soil transfer likely had only a small effect on soil water dynamics because both sites received similar amounts of precipitation during the incubation period (Table 1), and postincubation water contents of paired soils incubated *in situ* or transferred to the other site were similar. Assuming a minimum of a two-fold increase in net N transformation rates and a soil temperature increase of 3.9 °C when transferring soil from the high- to the low-elevation site, we calculate a Q_{10} greater than 6 for these soil processes. This Q_{10} value is one of the highest reported in the literature for soil net N transformations measured under controlled laboratory conditions (Kirschbaum 1995).

Using a similar experiment design, Jonasson *et al.* (1993) also found a more than doubling in the growing season net N mineralization rate after transferring the soil humus layer of a dwarf shrub (*Cassiope tetragona*) community from a high-elevation fellfield to a lower elevation subarctic heath in Sweden. The heath site had a 4.1 and 1.3 °C higher mean air and soil temperature than the fellfield site, respectively. However, in contrast to our results, transferring soils from the low- (heath) to the high-elevation site (fellfield) did not significantly reduce net N mineralization rates, which were already very low *in situ*. Furthermore, net nitrification was not observed in any soil treatment. Jonasson *et al.* (1993) also manipulated temperature under field conditions using greenhouses at both sites that provided temperature increases similar in magnitude as the reciprocal soil-transfer experiment; however, these greenhouse temperature manipulations did not result in significant increases in net N mineralization. The authors did not explain why these two different approaches of simulating climate change produced different effects on net N mineralization, but they concluded that soil temperature increases up to 2 °C will have only small effects on net N mineralization in subarctic tundra soils.

In another manipulative experiment using buried heating tapes in a mixed deciduous forest in northeastern USA, Peterjohn *et al.* (1994) reported a doubling of net N mineralization rates over the growing season in the forest floor and surface mineral soil (upper 13 cm) in plots where the soil temperature was increased by 5 °C (at 4-cm depth). Heating had no effect on net nitrification, which was low for both heated and control soils throughout their study. Soil heating had no apparent effect on inorganic N leaching below the plant rooting zone in their study (measured by tension lysimeters at 50 cm depth); in the presence of plant uptake, inorganic N losses from leaching were low in both heated and control plots. Their results suggest that the increased inorganic-N leaching values that we observed in our soil transfer simulation of climate change are probably the result of the prevention of plant N uptake from the confined soil cores.

However, over time, sustained increases in available N due to global warming may eliminate N-limitation in both plants and soil microflora (Hart & Stark 1997), resulting in increases in N loss by leaching. This scenario is exemplified in preliminary results from a soil warming experiment being conducted in southern Norway, at a site that is not N-limited because of high amounts of N entering the ecosystem from atmospheric deposition (Lükewille & Wright 1997). In this catchment-scale study, a 3–5 °C increase in surface soil temperature resulting from heating tapes has increased NO_3^- and NH_4^+ concentrations in runoff in the first year of treatment. However, short-term increases in available N due to faster rates of N cycling associated with global warming may simply result in more rapid depletion of labile organic-N pools within the soil, eventually again resulting in an N-limited ecosystem.

Limitations of soil transfer methodology as a climate change analogue

In this study, we have shown that the use of a combination of reciprocal soil transplants along altitudinal gradients and laboratory incubations under controlled conditions provides a powerful, cost-effective tool for predicted the potential effects of climate change on soil processes. However, all experimental methods have their inherent limitations. For instance, experimental manipulations (including the soil transfer approach presented here) simulate climate change by more-or-less instantaneously increasing temperature, rather than the slow increase in global temperature that is predicted to occur. Instantaneous increases in temperature will likely have much different effects on ecosystem processes than similar magnitude changes over extended period of time, because of the ability of organisms to adapt, immigrate to, or emigrate from the changing conditions (Perry *et al.* 1990). Only through the use of ecosystem models (e.g. Pastor & Post 1988; Rastetter *et al.* 1991) can we simulate potential changes over short time periods; how-

ever, experimental manipulations are necessary to parameterize and constrain these models.

One obvious limitation of the soil transfer experimental approach described here is that plants are not included in the climate change simulation. The removal of potentially important soil microorganism–plant interactions (Perry *et al.* 1990; Kaye & Hart 1997) and soil-plant ecosystem feedbacks (Pastor & Post 1988; Zak *et al.* 1993) from the experimental system may result in artifactual results. With small-statured plants (e.g. shrubs, grasses, tree seedlings), it would be possible to adapt our approach to include plants within the soil core being transferred, but this is not possible for large individuals such as the old-growth trees dominating our study sites. Hence, soil transfer studies as a surrogate experiment system of climate change are only useful for augmenting, but not replacing, large-plot or catchment-level temperature manipulation field experiments.

Conclusions

Because we exchanged soils between only two forest stands, we are unable to generalize our results to other old-growth conifer forests of the US Pacific Northwest. Further, we did not assess the effect of altitudinal transfer on N cycling within the forest floors of these stands, where tree fine-roots also are relatively abundant and which also contain important stores of plant-available N (Sollins *et al.* 1980). Our results support the hypothesis that high-elevation, old-growth forest soils in the central Cascades have higher C and N storage than their low-elevation analogues primarily because low temperatures limit net C and N mineralization rates at higher elevations. Hence, increases in surface temperatures associated with global warming will likely increase net rates of C and N mineralization from these high-elevation forest soils. However, it is unclear if the additional amounts of mineralized soil C and N will contribute to increases in global warming (from increased emissions of CO_2 or N_2O) and eutrophication of downslope aquatic ecosystems (from increased inputs of N to N-limited streams), or if concomitant increases in net primary production will sequester all or part of the released C and N. Experimental evidence from arctic tundra ecosystems suggests that net primary productivity is less temperature-limited than soil microbial activity (Shaver *et al.* 1992), implying that at least some of the global warming-released soil C and N will have an impact on atmospheric and aquatic systems.

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