

## ORIGINAL ARTICLES

# Nitrogen Mineralization in Two Unpolluted Old-Growth Forests of Contrasting Biodiversity and Dynamics

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## ABSTRACT

Studies in unpolluted, old-growth forests in the coastal range of southern Chile (42°30'S) can provide a baseline for understanding how forest ecosystems are changing due to the acceleration of nitrogen (N) inputs that has taken place over the last century. Chilean temperate forests, in contrast to their northern hemisphere counterparts, exhibit extremely low losses of inorganic N to stream waters. The objectives of this study were (a) to determine whether low inorganic N outputs in these forests were due to low rates of N mineralization or nitrification, and (b) to examine how biodiversity (defined as number of dominant tree species) and forest structure influence N mineralization and overall patterns of N cycling. Studies were conducted in a species-poor, conifer-dominated (*Fitzroya cupressoides*) forest with an even-aged canopy, and in a mixed-angiosperm (*Nothofagus nitida*) forest with a floristically more diverse and unstable canopy. Nitrogen mineralization rates measured in laboratory assays varied seasonally, reaching 6.0 µg N/g DW/day in both forests during late summer. Higher values were related to higher microbial activity, larger pools of labile inorganic N, and increased fine litter inputs. Field assays, conducted monthly, indicated positive net flux from N mineralization mainly from December to January in both

forests. Annual net flux of N from mineralization varied from 20 to 23 kg/ha/year for the *Fitzroya* forest and from 31 to 37 kg/ha/year for the *Nothofagus* forest. Despite low losses of inorganic N to streams, N mineralization and nitrification are not inhibited in these forests, implying the existence of strong sinks for NO<sub>3</sub><sup>-</sup> in the ecosystem. Field N mineralization rates were two times higher in the *Nothofagus* forest than in the *Fitzroya* forest, and correlated with greater N input via litterfall, slightly higher soil pH, and narrower carbon (C)–nitrogen ratios of soils and litter in the former. Differences in N mineralization between the two forest types are attributed to differences in biotic structure, stand dynamics, and site factors. Median values of net N mineralization rates in these southern hemisphere forests were lower than median rates for forests in industrialized regions of North America, such as the eastern and central USA. We suggest that these high N mineralization rates may be a consequence of enhanced atmospheric N deposition.

**Key words:** net N mineralization; nitrification; temperate forests; *Fitzroya*; *Nothofagus*; laboratory soil incubations; in situ soil incubations; seasonal patterns.

## INTRODUCTION

There are major uncertainties in our understanding of how forest ecosystems will respond to the acceleration of nitrogen (N) inputs that has taken place

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over the last century [for example, see Vitousek (1994), Hedin (1994), Howarth and others (1996), and Vitousek and others (1997)]. Enhanced N inputs can bring unpredictable consequences for how forests function as biogeochemical systems, such as increased N export to downstream ecosystems (Aber 1992; Durka and others 1994; Howarth and others 1996), long-term acidification and depletion of plant-available base cations from soils (Likens and others 1996; Hedin and Likens 1996), reduced tree growth in sensitive forests (Aber and others 1995), and changes in biotic structure (Schulze and others 1989). Since many forest ecosystems are N limited, N inputs can also trigger increased fixation of atmospheric carbon dioxide at rates that may be of consequence for the global carbon (C) budget [for example, see Schindler and Bayley (1993) and Townsend and others (1996)].

Despite the importance of understanding how human activities are changing the forest N cycle, the mechanisms and extent of change are difficult to determine in areas that are simultaneously affected by chronic N deposition, regional deforestation, and/or other forms of human disturbance. Studies of primary forests in areas with low or negligible air-pollution N inputs can provide valuable baseline information on the paths and kinetics of N cycling in forested ecosystems that are minimally impacted by humans. Such information may offer new insights into how forests functioned as biogeochemical systems in preindustrial conditions and may provide baseline information—or a *null model*—against which modern human effects on the N cycle can be better understood and evaluated (Hedin and others 1995).

Of further general interest is the question of how differences in biodiversity of natural communities affect ecosystem functions such as patterns of N cycling. Recent work on this topic has emphasized N cycling in plant communities that have been designed by human experimenters (Tilman and others 1996). However, studies of how N cycles depend on variations in biodiversity in natural, anthropogenically undisturbed, systems are few or lacking. The plant communities in our study area enable us to address this question directly.

Our study focuses on old-growth, temperate evergreen rain forests at the Cordillera Piuchú Ecosystem Study (CPES) on the Pacific Coast of southern South America (42°30'S). These forests are in contact with one of the cleanest atmospheres in the world, and atmospheric deposition is dominated by dilute sea-salt aerosols delivered by persistent westerly winds from the southern Pacific Ocean (Hedin and others 1995; Galloway and others 1996).

We showed previously (Hedin and others 1995) that the N cycle in CPES forests differs considerably from that of temperate forests in more polluted regions of the northern hemisphere. Old-growth CPES forests exhibit very low losses of inorganic N in watershed streams, with levels of  $\text{NO}_3^-$  (part per trillion) and ratios of  $\text{NO}_3^-$ -N: $\text{NH}_4^+$ -N (0.02–0.5) that, to our knowledge, are the lowest reported from any temperate old-growth forests. And yet, CPES forests leak considerable amounts of N in the form of dissolved organic N (DON; representing more than 95% of total dissolved N loss). These patterns of N loss may have important implications for our understanding of nutrient limitation in unpolluted forests. We hypothesized (Hedin and others 1995) that DON losses may control the N cycle in these forests and may provide a mechanism that can keep forests N limited over very long periods. Recent modeling efforts (Vitousek and others 1997) provide theoretical support for this hypothesis.

To understand the “unpolluted” N cycle in CPES forests, we sought to investigate how the pattern of hydrologic N loss (high DON but low dissolved inorganic N) depends on the internal N cycle. Are losses of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  low because internal supplies of biologically available N (that is, by N mineralization) are closely balanced by biotic demand for N? Is the  $\text{NO}_3^-$ : $\text{NH}_4^+$  ratio low because of a lack of production of  $\text{NO}_3^-$  by nitrification, as previously proposed to be the case in some old-growth forests [by Rice and Panholty (1972), but see Robertson and Vitousek (1981) and Stark and Hart (1997)].

While there is increasing interest in understanding how biotic structure and diversity are linked to biogeochemical cycles (Pastor and Post 1986; Mladenoff 1987; Peet 1992; Tilman and others 1996), it has proven especially difficult to study this link in unpolluted and primary forest ecosystems. Our study forests range from diverse and productive angiosperm *Nothofagus*-type forests to less diverse and less productive gymnosperm forests that are dominated by *Fitzroya cupressoides* (Armesto and others 1995, 1996). Whereas the regeneration cycle of the *Nothofagus* forest is dominated by gap-phase dynamics, *Fitzroya* forests regenerate after large-scale, stand-disrupting disturbance events (Armesto and others 1996).

The unpolluted condition and contrasting biotic structure of different CPES forests provides us with a unique opportunity to investigate the following questions:

1. Why are losses of dissolved inorganic N so low in CPES forests? Are low losses a consequence of a

“slowly turning” internal N cycle, characterized by low rates of N mineralization? Or, alternatively, are losses low because the N cycle is “finely tuned,” with higher rates of N mineralization and nitrification that are retained efficiently by biotic uptake?

2. Why is  $\text{NO}_3^-$  only 1%–6% of hydrologic losses of inorganic N, and only 0.06%–0.2% of total dissolved N? Are low  $\text{NO}_3^-:\text{NH}_4^+$  ratios caused by a lack of nitrification? Or, alternatively, are low  $\text{NO}_3^-:\text{NH}_4^+$  ratios caused by efficient retention of  $\text{NO}_3^-$  within the forest ecosystem?

3. How is the internal N cycle related to forest structure and dynamics? How do community-specific factors such as floristic diversity, seasonality, and carbon-nitrogen (C/N) ratios of litterfall, or canopy turnover interact with the internal N cycle? Of particular interest is the comparison between floristically less diverse conifer forests with a stable canopy versus floristically richer angiosperm-dominated forests with a higher canopy turnover.

4. How do rates of internal N cycling (N mineralization and nitrification) in unpolluted CPES forests compare with other temperate forests in industrialized regions of the northern hemisphere that receive enhanced atmospheric N deposition?

## STUDY SITES

This study was conducted in montane coastal forests (550–680 m above sea level) in the Cordillera de Piuchué in Chiloé National Park (42°30'S), about 3–4 km east of the Pacific Ocean in Chiloé Island, southern Chile. The area is characterized by a wet-temperate climate with strong oceanic influence. Some weak seasonality in temperature and precipitation is characteristic, with rainy and cold winters extending from June to August, and warmer and less humid summers from December to March. During summer, the eastern Pacific high-pressure cell is displaced southward from its normal position at 30°S, causing decreased intensity and frequency of precipitation and periods of up to 1 month without rain. During winter, occasional windstorms or snowfall can cause extensive damage and multiple tree falls in the weaker canopies of angiosperm-dominated forests. Annual precipitation, recorded from April 1994 to March 1995, was estimated at about 620–730 cm with about 10%–15% falling during summer. Average winter temperature (July–September 1994) was 4.2°C, and average summer temperature (January–March 1995) was 10.2°C.

Flat summits of the CPES mountain range (600–700 m above sea level) are dominated by a mosaic of forest and moorlands (Ruthsatz and Villagrán 1991), with cushion plants and sedges growing on poorly

drained soils or in the most exposed sites. Gentle, north-facing slopes (10°–30°) contain dense gymnosperm forests of *Fitzroya cupressoides* and *Pilgerodendron uviferum* (both Cupressaceae) with only low abundance of angiosperms such as *Nothofagus nitida*. Average canopy height is 15–18 m. On steeper (30°–40°) south-facing slopes and at altitudes of about 500–600 m, forests are dominated by broad-leaved evergreen trees that include *Nothofagus nitida* (Fagaceae), *Drimys winteri* (Winteraceae), and *Laureliopsis philippiana* (Monimiaceae), together with the narrow-leaved conifers *Podocarpus nubigena* and *Saxegothaea conspicua* (both Podocarpaceae) and various species of the woody Myrtaceae (Armesto and others 1995, 1996). Average canopy height is about 30 m, with some emergent *Nothofagus* trees reaching up to 35 m (Armesto and others 1995). Preliminary records of environmental variables indicate some minor differences between *Fitzroya* and *Nothofagus* forests. The levels of photosynthetically active radiation reaching the canopy are the same in both forests. Nevertheless, the lower altitude of *Nothofagus* forest and the greater exposure to northwest winds of the *Fitzroya* forest result in small differences in the annual ranges of air temperatures (0°–25°C in *Nothofagus* forest versus –1° to 28°C in *Fitzroya* forest). Soil temperatures are also slightly higher in the *Nothofagus* forest than in the *Fitzroya* forest (3.2°–13.3°C versus 2.5°–12.4°C, respectively). Soil moisture values are similar in both forests (73%–87% for *Nothofagus* and 81%–88% for *Fitzroya* forest).

Forest soils are underlain by a highly weathered, impermeable, Paleozoic micaschist (Holdgate 1961; Pérez and others 1991; Ruthsatz and Villagrán 1991). Both forests grow on cambisols (FAO–UNESCO 1974) 40–60 cm deep, with a high content of organic matter (about 50%  $C_c$ ) in the upper 10 cm. Soils are acidic (pH < 5) and have low base-cation contents with an average of 15  $\text{cmol}_c/\text{kg}$  soil of exchangeable calcium (D. Zarin and others unpublished data).

## Forest Dynamics and Canopy Composition

The canopy of angiosperm-dominated *Nothofagus* forest has a greater tree species diversity and higher equitability than the conifer-dominated *Fitzroya* forest (Table 1). The equitability index ( $E_c$ ) was defined by Whittaker (1975) as

$$E_c = S/\log_{n_1} - \log_{n_s}$$

where,  $S$  is the number of tree species,  $n_1$  is the largest frequency value of a species in the sample unit, and  $n_s$  is the smallest frequency value of a species in the sample unit.

**Table 1.** Species Diversity and Structural Characteristics of Two Montane Forests in Cordillera de Piuchué, Chiloé, Chile

	Forest Type	
	<i>Fitzroya</i>	<i>Nothofagus</i>
1. Number of dominant canopy species	2	5
2. Equitability index	3.7	4.7
3. Living-tree density (trees/ha) <sup>a</sup>	2438	1725
4. Snag density (trees/ha) <sup>a</sup>	1788	425
5. Medium-sized woody debris (kg/ha) <sup>a</sup>	440 ± 80	3660 ± 1740
6. Basal area (m <sup>2</sup> /ha)	167	82

<sup>a</sup>From J. J. Armesto, C. A. Pérez, and M. R. Carmona (unpublished manuscript).

The *Fitzroya* forest is characterized by higher densities of both snags and living trees, and a basal area twice as high as that of *Nothofagus* forest (Table 1). The *Fitzroya* forest also displays less biomass of medium-sized woody debris (1- to 5-cm diameter) than the *Nothofagus* forest (Table 1). Field observations indicate that conifers tend to decay standing (J. J. Armesto, C. A. Pérez, and M. R. Carmona unpublished data), and *Fitzroya* is known for its highly resistant and slowly decaying wood. Sampling of permanent 40 × 20-m plots in 1989 and 1996 showed that no canopy trees had died in the *Fitzroya* forest, whereas 11% of the living stems [greater than 5 cm in diameter at breast height (DBH)] died and 81% of the snags fell down in the *Nothofagus* forest during the same period (J. J. Armesto and others unpublished data). *Fitzroya* forests thus generally have a stable canopy, in contrast with angiosperm-dominated *Nothofagus* forests, which display less stable canopies with frequent tree falls, primarily caused by wind.

Reflecting their differences in dynamics, the two forest types also have sharply contrasting DBH structures (Armesto and others 1995, 1996). The dominant canopy trees in *Nothofagus* forests are the relatively shade-intolerant *Nothofagus nitida* and *Drimys winteri*, both of which regenerate in medium to large tree-fall gaps and have bimodal or multimodal DBH distributions with only limited regeneration under the canopy (Armesto and others 1996). In contrast, the dominant species in conifer forests, *Fitzroya cupressoides*, is shade intolerant and displays a unimodal, bell-shaped DBH distribution with a complete absence of saplings or seedlings. This suggests that a single cohort of trees regenerated

following a stand-disrupting event. Dendrochronological data (J. C. Aravena and J. J. Armesto unpublished data) indicate a modal age of 450 years (range, 350–500 years) for the canopy trees in the conifer forest studied.

## METHODS: NITROGEN MINERALIZATION AND NITRIFICATION

### Laboratory Incubations

We determined potential N mineralization and nitrification by laboratory incubations. Three samples of surface soil (Ah horizon, first 10 cm) were taken at random locations in each forest type from June 1994 to April 1995 (every other month during autumn, winter, and spring). Additional samples were taken in October 1995 and in May 1996. Samples were sieved through a 2-mm-mesh screen, homogenized, and combined into one sample per forest type. For each forest type, three subsamples of the homogenized soil were used to determine initial contents of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> (see below). In addition, 27 subsamples per forest type and sampling period were placed in plastic bags (permeable to gas exchange, but impermeable to water) and incubated for up to 31 days in a controlled-environment chamber at a constant temperature of 20°C (Zottl 1958; Campbell and others 1993). During the first 2 weeks of the incubation, samples were retrieved from the chamber approximately every other day, with three replicates per forest type. During the last 2 weeks of the incubation, samples were retrieved approximately every 5 days, also with three replicates per forest type. Consequently, we had nine sample times for each incubation (from  $t = 0$  to  $t = 30$  days). Moisture content of samples throughout the laboratory incubation assays was similar to field conditions (75%–80%).

### Field Incubations

Field incubations were conducted in conifer (*Fitzroya*) and angiosperm (*Nothofagus*) forests using the “buried bag method” (Eno 1960) from May 1994 to May 1996. The experiment was limited to the Ah horizon (0- to 10-cm depth) because field observations indicated that fine-root biomass in both forests is concentrated in the first 10 cm of the soil profile. This suggests that most of the microbial activity and plant uptake of nutrients occur in this soil horizon. In both forest types, the total depth of the O horizon (Ol, Of, and Oh) is about 5 cm, but its high C/N ratio (>45) suggests that microbial activity and decomposition processes in the litter layer may be very limited. Below 10 cm, fine roots are scarce,

whereas medium-sized and coarse anchoring roots dominate the soil profile. We assumed that microbial activity and plant uptake below 10 cm is a small proportion of the total activity in the soil profile.

Three samples of surface soil (Ah horizon, <10 cm) were collected from random locations inside three 5 × 10-m plots in each forest type. Samples were sieved and homogenized, and three samples per plot were taken to the laboratory to determine initial amounts of exchangeable  $\text{NH}_4^+$  and  $\text{NO}_3^-$  (see below). A second set of three samples per plot was returned to the soil profile inside semipermeable plastic bags. After approximately 30 days, the nine samples (three per plot) were retrieved from each forest and taken to the laboratory to determine production of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  under field conditions. Three values were averaged to obtain one value of N mineralization per plot. Soil moisture was measured in all samples. The sample for July 1995 (not shown in graphs) is missing because the site was inaccessible due to a thick snow cover that lasted for 3–4 weeks. The annual amount of N mineralized that is available for plant uptake in surface soil (0–10 cm) was calculated by adding up all positive values of monthly net N mineralization, after subtracting the amount of N immobilized by microbes or abiotically (given by negative values of net N mineralization). Values were expressed relative to 1 ha, based on an estimated bulk density for both forest soils of 100 Mg/ha (Pérez and others 1991; A. Johnson and others unpublished data).

### Soil Extraction and Chemical Analyses

Ammonium and  $\text{NO}_3^-$  were extracted from initial and incubated soil samples in a 1:4 ratio of soil-solution of 0.021 mol/L  $\text{KAl}(\text{SO}_4)_2$  (Gerlach 1978). This suspension was mechanically shaken for 20 min and then filtered, 10 mL of the filtered clear solution with an excess of MgO was steam distilled in a micro-Kjeldahl apparatus to obtain  $\text{NH}_4^+$  as  $\text{NH}_3$ . Nitrate in the solution was reduced to  $\text{NH}_3$  by adding 1 mg of Devardas Alloy. Both contents were determined through titration with a solution 0.005 N  $\text{H}_2\text{SO}_4$  from a microburette. The amounts of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  produced were added to obtain the total N mineralized ( $N_{\text{min}}$ ) in each incubation (Runge 1974; Gerlach 1978). Relative nitrification was taken as the proportion of nitrate to total mineralized N.

Soil pH was measured with a glass electrode in a 1:2 proportion of soil-to-distilled water. Total organic C and N were determined by a C–N Analyzer (Carlo Erba Instruments) in 10 samples of surface soil (<10-cm depth) that were sieved and ground for each forest type.

### Quantitative Analyses

Two different kinetic models were used to quantify potential N mineralization ( $N_{\text{min}}$  = cumulative N mineralized in  $\mu\text{g N/g}$  dry soil) in laboratory-incubated soil samples (Standford and Smith 1972; Paustian and Bonde 1987; Ellert and Bettany 1988; Fyles and others 1990; Campbell and others 1993):

$$\text{Linear regression: } N_{\text{min}} = kt + b \quad (1)$$

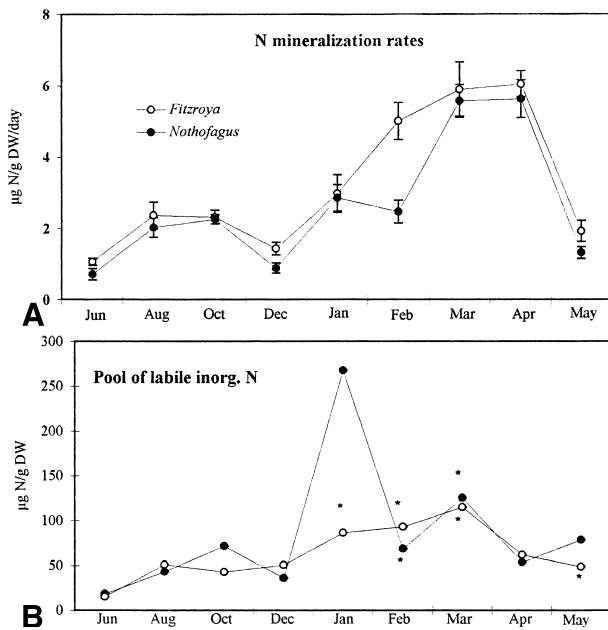
$$\text{First-order equation: } N_{\text{min}} = N_0[1 - \exp(-kt)], \quad (2)$$

where  $k$  is the mineralization rate constant ( $\text{days}^{-1}$ ),  $b$  is the intercept and,  $t$  is the time (days), and  $N_0$  is the pool of potentially mineralizable N (when time tends to infinite the value of  $N_0 = N_{\text{max}}$ ; the maximum amount of N mineralized; the asymptote of the curve). The most appropriate model varied as a function of season. For each sample event, we selected the model that yielded the highest  $r^2$  value. To compare  $k$  values between conifer and angiosperm forests, we calculated linear regressions for the first 8 days of each incubation. We estimated the total pool of labile inorganic N present in the soil sample either from  $N_0$  in Eq. 2, or from the final concentration of mineralized N, after each 30-day incubation. Although all samples from a forest were pooled prior to each incubation ( $n = 1$ ), we interpret the differences observed between forests as being representative of the two forest types.

“In situ” net N mineralization was calculated from the net change in exchangeable  $\text{NH}_4^+$  and  $\text{NO}_3^-$  between initial and final samples for each field plot. We used analysis of variance (ANOVA) to compare field N mineralization rates, litterfall input, C/N ratios of soil, and pH values between the two forest types. Values for each plot were considered as replicates ( $n = 3$  plots per forest type). Although each forest type contained replicate plots, the two forests were by necessity located in two different areas of the landscape. Thus, our statistical treatment (forest type) does not comply with the assumption of replicate plots that are “randomly located” in the landscape. Although this does not invalidate assignment of statistical significance, it introduces some difficulty in discriminating effects, due to differences between forest types or differences due to other landscape-level factors. Given the strong coupling between forests and their soil environment, we believe that effects due to forest type dominate our analyses.

### Fine Litterfall

Between May 1995 and May 1996, fine litterfall was collected in 16 litter collectors in the *Fitzroya* forest



**Figure 1.** A Annual trends of nitrogen mineralization rates, based on  $k$  (mineralization rate constant) values derived from the best-fit model for the relationship of nitrogen (N) mineralization over time, during laboratory incubations of surface soils of *Fitzroya* and *Nothofagus* forests. Bars are 1 SE of the mean of three replicate subsamples per forest type. B Pools of labile inorganic N produced each month in laboratory incubations of *Fitzroya* and *Nothofagus* forest soils, estimated as the maximum or the asymptotic value of the relationship of N mineralization over time. \*Months when N mineralization followed a linear model; DW, dry weight.

and 12 litter collectors in the *Nothofagus* forest. The collectors were placed randomly along transect lines from the top to the bottom of the slope. Each collector consisted of a 0.5-m-diameter funnel made of a plastic 1-mm-mesh sieve positioned vertically 1 m from the ground. The collectors were emptied each month, and samples were taken to the laboratory to determine dry weight and separated by species. C and N contents were determined by a C-N Analyzer at the University of Pennsylvania. We used one-way ANOVA and Tukey's tests to compare C/N ratios of litter-fall between dominant tree species in each forest type.

## RESULTS: NITROGEN MINERALIZATION IN SOILS

### Laboratory Incubations

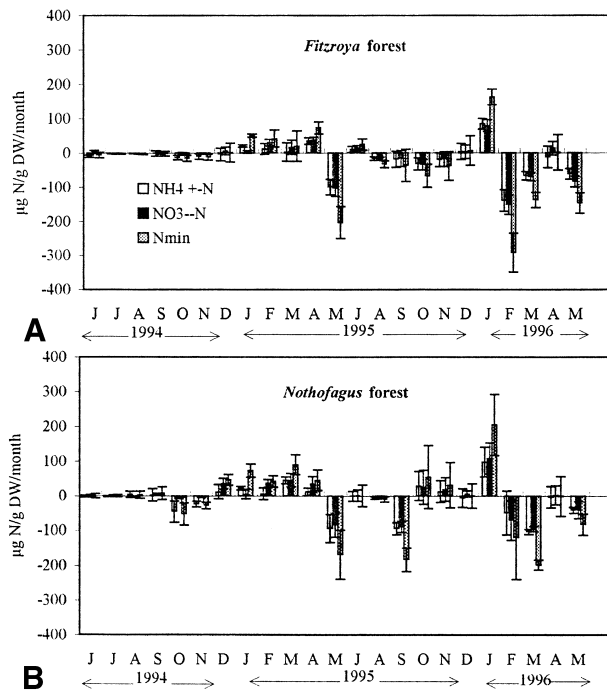
Rates of potential N mineralization showed a pronounced seasonality, reaching a maximum of 6.0 µg

N/g dry weight (DW)/day in both forests in the warm and dry late-summer early-fall period (February–April) (Figure 1A). Rates were lowest during the colder and wetter period between late winter (June) and early spring (December). Potential N mineralization followed a first-order model during most of the year in both forest types, except for February and March (midsummer to late summer), during which a linear model was most appropriate (indicated by stars in Figure 1B). In the *Fitzroya* forest, a linear model was also the best-fit model for January and May (Figure 1B). The fit to a first-order model suggested the presence of a limited pool of labile inorganic N available in the soil for microbial decay. The largest pool size of labile inorganic N was reached during January in the *Nothofagus* forest (Figure 1B), while in the *Fitzroya* there was a weak trend of greater pools of labile inorganic N from midsummer to late summer (January–March, Figure 1B).

### Field Nitrogen Mineralization

During 2 years of sampling, we found strong seasonal variations in the fluxes of N from mineralization. In both forest types, positive mineralization rates, indicating N that is available for plant uptake, occurred during the warmest and driest summer months (December and January) in the 2 years of study (Figure 2). Negative values, indicating different degrees of immobilization of N, either biotic or abiotic, occurred at various times during the rest of the year.

Adding positive monthly values of net N mineralization, we calculated the annual net flux of mineralized N for plant uptake in the *Nothofagus* forest to be  $31.4 \pm 3.7$  kg/ha/year (mean  $\pm$  SD) from May 1994 to May 1995 and  $37.2 \pm 8.9$  kg/ha/year from June 1995 to May 1996. For the *Fitzroya* forest, the annual net flux of mineralized N for plant uptake was  $19.8 \pm 9$  kg/ha/year from May 1994 to May 1995 and  $23 \pm 6.2$  kg/ha/year from June 1995 to May 1996. ANOVA indicated that annual net flux of N from mineralization differed between forests in the 2 years of study, but there was no difference between years ( $P = 0.015$  for the effect of forest type, and  $P = 0.32$  for the effect of year). Available N contents in forest soils ranged between 24 and 524 µg/g dry soil for *Fitzroya* and between 18 and 453 µg/g dry soil for *Nothofagus* forest during the 2 years of study. From these data, we estimated a pool of available soil N that ranged between 2 and 52 kg/ha for *Fitzroya* forest and between 2 and 45 kg/ha for *Nothofagus* forest.



**Figure 2.** Monthly variation of total nitrogen mineralization, ammonification and nitrification rates obtained from field incubations of soils conducted from May 1994 to May 1996 in *Fitzroya* A and *Nothofagus* B forests. Values shown are means  $\pm 1$  SD ( $n = 9$  samples per month). DW, dry weight.

**Table 2.** Relative Nitrification (% Total Nitrogen Mineralized) in Laboratory and Field Incubations of CPES Forest Soils

Forest Type	Laboratory	Field
<i>Fitzroya</i>	50 $\pm$ 1	54 $\pm$ 23
<i>Nothofagus</i>	50 $\pm$ 1	62 $\pm$ 24

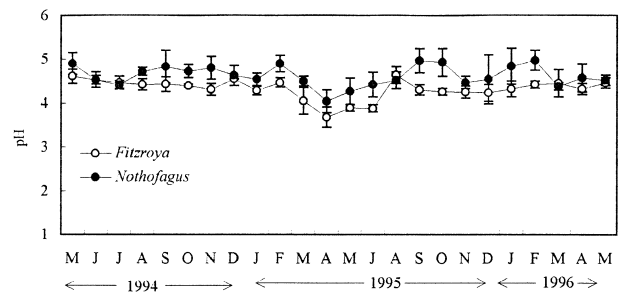
CPES, Cordillera Piuchué Ecosystem Study.

**Nitrification**

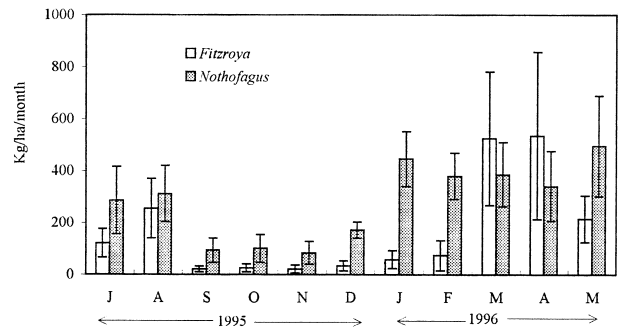
For both conifer and angiosperm forest types, relative nitrification was high in both laboratory and field incubations. Nitrification was consistently near 50% of total N mineralization (Table 2), indicating that nitrifying microorganisms are very active in CPES forest soils.

**pH Values and Water Content in Soils**

Soil pH values remained relatively stable in both forest types (Figure 3), but were consistently lower ( $P < 0.0001$ , ANOVA) in the *Fitzroya* forest (mean = 4.3, SE = 0.2,  $n = 24$ ) than in the *Nothofagus* forest (mean = 4.6, SE = 0.2,  $n = 24$ ). Field soil moisture contents ranged from 76% to 87% throughout the 2



**Figure 3.** Monthly course of soil pH values in *Fitzroya* and *Nothofagus* forests from May 1994 to May 1996. Values shown are means  $\pm 1$  SD ( $n =$  samples per site/month).



**Figure 4.** Monthly variation of fine-litter input in the *Fitzroya* ( $n = 16$  traps/month) and *Nothofagus* ( $n = 12$  traps per month) forests from May 1995 to May 1996. Values shown are means  $\pm 1$  SD.

years of study, indicating that soil moisture conditions remained favorable for soil microbial activity.

**Fine-Litterfall Dynamics**

Inputs of fine litterfall to the soil of *Fitzroya* and *Nothofagus* forests showed similar seasonal patterns (Figure 4). Inputs were low in spring (September–December) and increased from midsummer to early fall. There was a marked increase in litterfall in March and April in the *Fitzroya* forest and from January to May in the *Nothofagus* forest. The accumulated annual input of litter from May 1995 to May 1996 was significantly lower ( $P < 0.0001$ , ANOVA) in the *Fitzroya* forest ( $1743 \pm 692$  kg/ha/year) than in the *Nothofagus* forest ( $3039 \pm 625$  kg/ha/year). These values represent estimated fluxes of N of 10.7 kg/ha/year to *Fitzroya* forest and 22.6 kg/ha/year in *Nothofagus* forest.

**Carbon–Nitrogen Ratios in Soil and Fresh Litter**

Our analyses of total C and N in surface soil showed narrower C/N ratios in the soil of *Nothofagus* forest (33.4) than in the *Fitzroya* forest (39.0) ( $P < 0.0001$ , ANOVA). In both litterfall samples, canopy species

**Table 3.** Carbon–Nitrogen Ratios of Fresh Litter of Major Canopy Dominants in CPES Forests

Species	Sampling Period	
	May–June	June–August
Mixed forest		
<i>Nothofagus nitida</i>	128.9 ± 9.3 <sup>a</sup> (n = 9)	61.0 ± 0.8 <sup>a</sup> (n = 5)
<i>Drimys winteri</i>	65.4 ± 4.4 <sup>b</sup> (n = 4)	53.9 ± 3.4 <sup>a</sup> (n = 5)
Other canopy species	53.4b ± 0.5 <sup>b</sup> (n = 2)	46.3 ± 7.9 <sup>a</sup> (n = 3)
Conifer forest		
<i>Fitzroya cupressoides</i>	110.7 ± 2.7 <sup>c</sup> (n = 2)	108.2 ± 8.6 <sup>b</sup> (n = 4)

CPES, Cordillera Piuchué Ecosystem Study.  
For a given sampling period, values followed by different superscript italic letters are significantly different ( $P < 0.05$ , ANOVA, Tukey).

of *Nothofagus* had narrower C/N ratios than did species of *Fitzroya* forest, with the exception of *Nothofagus* litter during May–June (Table 3). The C/N ratio in fresh litter of *Nothofagus nitida* decreased to one-half of its value from May–June to June–August, suggesting a strong seasonal pattern.

## DISCUSSION

### Nitrogen Mineralization and Nitrification

CPES forest soils showed high rates of potential N mineralization, and about 50% of the mineralized N in these assays was in the form of nitrate. The highest potential net N mineralization rates (6 µg N/g dry soil/day) measured in laboratory incubations of Chilean forest soils were higher than rates of 1–2 µg/dry soil/day reported for laboratory incubations of soils from North American temperate conifer and angiosperm forests (Robertson 1982, 1984; Vitousek and others 1982). Laboratory-incubated CPES soils show a potential N mineralization similar to that obtained in laboratory assays for soils of lowland and montane tropical forests (Tanner 1977; Chandler 1985; Vitousek and others 1983). Nitrogen mineralization rates estimated from laboratory assays and the pools of labile inorganic N in soils increase toward the end of the warm season, presumably owing to both increments in microbial biomass and higher inputs of fresh litter, induced by the short dry period.

Because of the large differences between the rates of N production estimated from laboratory-incubated soil samples (up to 6 µg N/g DW/day) and those estimated from in situ incubations (up to 3 µg

N/g DW/day), we infer that low temperatures can be a significant constraint on N mineralization rates in the field. However, our results show that both mineralization and nitrification take place at relatively high rates in these forests at various times during the year, but particularly in late summer.

### Evidence for Inorganic Nitrogen Retention

Preliminary estimates of the annual input of inorganic N via precipitation to these coastal forests are on the order of 0.1 kg/ha/year, but the estimated outputs calculated from the concentration of inorganic N in stream-water samples are only ca. 0.4 kg/ha/year (L. O. Hedin unpublished data). Seasonal pulses of N mineralization and nitrification in forest soils during the period of this study did not result in significant exports of inorganic N to forest streams (Hedin and others 1995 and unpublished data). This result and the high ammonium-to-nitrate ratio in hydrologic outputs suggest that inorganic N, primarily in the form of nitrate, is strongly retained within the forest ecosystem, either in plant or in microbial biomass, where it is immobilized.

In this study, net flux of N from mineralization that becomes available for plant uptake in *Fitzroya* forest soil varied between 20 and 23 kg/ha/year. The annual amount of N required for new growth of trees in this forest was calculated by adding the estimated increase in bole-wood N, the amount of N required to replace N losses in litterfall, and the amount of N required for fine-root turnover [assumed to be the same as the amount of N required for growth of new foliage (A. Johnson and others personal communication)]. The calculated annual requirement of N for tree growth is 21 kg/ha/year. Assuming that the largest demand for N in this forest ecosystem is tree growth, the close balance between these two estimates becomes strong evidence for a very tight internal N cycle. According to preliminary analyses of throughfall in CPES forests, N leaching from the canopy in the *Fitzroya* forest appears to be negligible (K. C. Weathers personal communication).

Nitrate may also be efficiently retained within the soil compartment, where it may be available for plant uptake. Soil humus has a high capacity for exchanging anions through the variable charges that depend on soil pH (Sollins and others 1988). The high content of organic matter (up to 50% total C) and strongly acidic soils of CPES forests suggest that variable charge exchange complexes can contribute to the retention of plant-available N in these soils.

### Nitrogen Mineralization in Relation to Biodiversity, Stand Dynamics, and Site Characteristics

The annual rate of net N mineralization was higher in the *Nothofagus*-dominated angiosperm forest than in the *Fitzroya*-dominated conifer forest, and this difference is associated with slightly higher pH values, higher N inputs via litterfall, and narrower C/N ratios of surface soil and fresh litter of canopy dominants in the *Nothofagus* forest.

*Nothofagus* forests grow on steeper slopes, and canopy trees are more susceptible to windthrow than in *Fitzroya* forests (Armesto and others 1995, 1996). In addition, fine-litter inputs in *Nothofagus* forests derive from a variety of broad-leaved tree species with narrower C/N ratios (40–60) in fresh litter, even though for each species these ratios may show a strong seasonal variation. In contrast, *Fitzroya* forest is largely dominated by one species of conifer, *Fitzroya cupressoides*, with a comparatively higher C/N ratio (90–100) of fresh litter. These two factors in combination—biodiversity, as expressed in the species diversity of canopy trees, and stand dynamics—may lead to higher rates of N mineralization in soils of the *Nothofagus* forest, although losses of ammonium and nitrate via streams remain low in both forests (Hedin and others 1995). Canopy openings, associated with gap-phase dynamics, and higher inputs of N via fine litter in *Nothofagus* forest could enhance N mineralization, as shown under tree-fall gaps in North American temperate forests (Mladenoff 1987), and/or enhance demands on N by regrowing vegetation.

*Fitzroya* forests, in turn, have a more stable canopy and a longer regeneration cycle (more than 500 years) than *Nothofagus* forests in the Chilean coastal range (Armesto and others 1995; Lusk 1996). Consequently, N mineralization would be comparatively lower because of the low frequency of canopy gaps and more limited N inputs via litterfall.

Environmental variables between the forest types indicate lower minimum air and soil temperatures in the *Fitzroya* forest, but similar maximum temperatures. These differences may be caused by topographic factors such as altitude and exposure. The presence of fast-growing species, such as *Nothofagus nitida*, *Drimys winteri*, and *Podocarpus nubigena*, may be favored in sheltered and lower-elevation slopes as opposed to exposed slopes, which are dominated by conifer forests. Therefore, physical factors (for example, exposure and altitude) can interact with differences associated with biotic diversity, such as differences in litter quality and stand dynamics, to determine the higher net N flux from mineralization

observed in the *Nothofagus* forest. We suggest that a feedback mechanism between soil and plants, where C/N ratios of litterfall and gap-phase dynamics may play a key role, determines the persistence of this mosaic of forest types in the landscape.

In summary, the observed differences in the net flux of N from mineralization between these two forest types are consistent with their differences in biodiversity, as inferred from tree species diversity and stand dynamics, which in turn are affected by site factors. In regions subjected to enhanced anthropogenic N inputs to ecosystems, differences in net N mineralization between forests, due to contrasting floristic composition and biodiversity, cannot be separated from the effects of differences in N inputs from the atmosphere.

### Nitrogen Mineralization in Unpolluted Versus Polluted Forests

Field incubations of soils from conifer forests of the world, including polluted as well as unpolluted sites, located at different latitudes, with different climate, soil, and bedrock types, exhibit values of annual net N mineralization ranging between 9 and 125 kg/ha/year (Gosz 1981). Soils from a group of temperate forests located in eastern and central USA and Canada have a median value of annual net N mineralization of 70 kg/ha/year (Table 4). These estimates were obtained in a region of North America receiving some of the highest atmospheric N inputs in the world (Galloway and others 1994). In contrast, the median value of annual net N mineralization reported in this article for forests located on the island of Chiloé in southern Chile, one of the regions of the world with the lowest atmospheric N deposition (Weathers and Likens 1997), is 28 kg/ha/year. A third group of temperate forests, located in the Pacific Northwest of the USA, have a median value of annual net N mineralization rate of 12 kg/ha/year. Atmospheric N inputs in this region are some of the lowest in the Northern Hemisphere (Galloway and others 1994).

Most of the forest sites in North America listed in Table 4 are characterized by young soils, developed over glacial substrates, and presumably less weathered than CPES forest soils derived from Paleozoic bedrock. On these basis, we could predict that older soils of CPES forests, which have a longer history of organic matter accumulation, should exhibit higher net N mineralization than the younger soils of their North American counterparts, which have a shorter history of accumulation of organic matter.

CPES forest soils are characterized by a high content of total C (50%) and by a high C/N ratio (33). In contrast, northern temperate forests of

**Table 4.** Field Estimates of Annual Net Nitrogen (N) Mineralization in Soils of North and South American Old-Growth Temperate Forests

Forest type	Location	Net N Mineralization (kg N/ha/year)	Reference
Eastern/central USA and Canada			
Spruce–Fraser fir	Appalachians	103	Strader and others (1989)
Maple	Upper Michigan	102	Mladenoff (1987)
Oak	Wisconsin	101	Nadelhoffer and others (1982)
Hemlock	Upper Michigan	89	Mladenoff (1987)
Red pine	Massachusetts	80	Aber and others (1993)
White pine	Wisconsin	80	Nadelhoffer and others (1982)
Sugar maple	Toronto	74	Hill and Shackleton (1989)
Hardwood	Massachusetts	71	Aber and others (1993)
White oak	Wisconsin	65	Pastor and others (1984)
White pine	Wisconsin	44	Pastor and others (1984)
Spruce–fir	Adirondacks	40	Friedland and others (1991)
Mixed oak	Central Ohio	39	Plymale and others (1987)
Red pine	Wisconsin	32	Nadelhoffer and others (1982)
Red pine	Wisconsin	26	Pastor and others (1984)
White pine	Toronto	23	Hill and Shackleton (1989)
	<i>Group median</i>	71	
CPES forests			
<i>Nothofagus</i> forest	Chiloé, Chile	34	This work
<i>Fitzroya</i> forest	Chiloé, Chile	22	This work
	<i>Group median</i>	28	
Pacific Northwest			
White fir	California	16	Hart and Firestone (1989)
Mixed conifer	Northern California	12	Frazer and others (1990)
Douglas fir	Oregon	6	Myrold and others (1989)
	<i>Group median</i>	12	

CPES, Cordilla Piuchué Ecosystem Study.

Values are means of different study sites. The median values for each regional group are also given.

eastern and central USA and Canada listed in Table 4 have lower total C contents (<16%) and lower C/N ratios (<24). Consequently, we suggest that the higher rates of net N mineralization obtained in temperate forests of eastern and central North America may be a direct consequence of enhanced regional rates of N deposition, possibly via long-term decreases in C:N ratios (see Aber 1992 and discussion below).

Other factors, such as differences in land-use history, may also affect the N mineralization rates in forest soils by altering the patterns of organic matter accumulation. Forests subjected to a long history of disturbance, either natural or anthropogenic, should exhibit limited rates of N mineralization because of depletion of the pools of organic matter in the soil, which represent the major source of inorganic N for the ecosystem in the absence of atmospheric N

deposition. For instance, the group of temperate forests of eastern and central USA and Canada that present N mineralization values below the median (Table 4) are known to have been historically affected by several processes that imply important losses of organic matter from the soil pool. This is the case of white pine and red pine forests located on alluvial terraces subjected to high erosion rates compensated by occasional deposition of sand (26–44 kg/ha/year) (Pastor and others 1984). White pine forest in Toronto, with a net N mineralization of 22 kg/ha/year (Table 4), are second-growth forests located on abandoned farmland (Hill and Shackleton 1989). Furthermore, red pine forests in the arboretum of the University of Wisconsin–Madison have a reported net N mineralization of 32 kg/ha/year (Table 4) and grow on alfisols presenting a conspicuous Ap horizon, which is evidence of inten-

sive land use before forest development. These examples indicate that land-use history contributes to reduced N mineralization rates despite the enhanced N deposition by depletion of the soil organic matter pool. In contrast, more pristine forests, such as old-growth CPES forests or Pacific Northwest forests, should maintain this organic matter pool.

On the other hand, net N mineralization values well above the median for North American temperate forests (Table 4) have been reported for two high-elevation forests of the Appalachian Mountains and the Adirondacks in the eastern USA. This region receives one of the highest inputs of atmospheric N in the world and exhibits symptoms of forest decline (Friedland and others 1991; Galloway and others 1994). A study by Friedland and colleagues (1991) in forests of the Adirondacks reports an extremely high rate of net N mineralization of 320 kg/ha/year in the mineral soil horizon, higher than the rate of 40 kg N/ha/year reported by these authors for the O horizon at this site (Table 4). These high values of net N mineralization are in conflict with predictions based on the topographic location, climate, and litter quality, which would place montane forests in the lowest range of net N mineralization rates.

In conclusion, this study supports Aber's (1992) hypothesis that chronic N deposition in some northern hemisphere forests has led to decreases in C/N ratios of soils and may have enhanced the rates of decomposition and mineralization of organic matter. In addition, we hypothesize that land-use history and disturbance in lowland forests of eastern North America have produced losses of N and C compounds from soil organic pools over time, thus leading to decreased rates of net N mineralization in relation to older montane forests. On the other hand, forests of Chiloé and the Pacific Northwest of North America, which have maintained or increased their pools of recalcitrant C and N associated with organic matter, have lower net N mineralization rates due to the lack atmospheric N input and higher C/N ratios. Additional research is needed to determine N mineralization rates in other unpolluted forests of the southern hemisphere, with differing climates, disturbance histories, and soils, so that these suggested patterns can be confirmed.

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