Austral Ecology (2003) **28**, 591–600

Litterfall dynamics and nitrogen use efficiency in two evergreen temperate rainforests of southern Chile

CECILIA A. PÉREZ,[1,2] JUAN J. ARMESTO,[1,2] CRISTIAN TORREALBA[1] AND MARTÍN R. CARMONA[1]
[1]*Laboratorio de Sistemática y Ecología Vegetal, Facultad de Ciencias, Departamento de Biología, Universidad de Chile, Santiago, Chile, and* [2†]*Center for Advanced Studies in Ecology and Biodiversity, P. Universidad Católica de Chile, PO Box 114-D, Santiago CP 6513677, Chile (Email: cperez@uchile.cl)*

Abstract In unpolluted regions, where inorganic nitrogen (N) inputs from the atmosphere are minimal, such as remote locations in southern South America, litterfall dynamics and N use efficiency of tree species should be coupled to the internal N cycle of forest ecosystems. This hypothesis was examined in two evergreen temperate forests in southern Chile (42°30′S), a mixed broad-leaved forest (MBF) and a conifer forest (CF). Although these forests grow under the same climate and on the same parental material, they differ greatly in floristic structure and canopy dynamics (slower in the CF). In both forests, biomass, N flux, and C/N ratios of fine litterfall were measured monthly from May 1995 to March 1999. There was a continuous litter flux over the annual cycle in both forests, with a peak during autumn in the CF. In the MBF, litterfall decreased during spring. In both forests, the C/N ratios of litterfall varied over the annual cycle with a maximum in autumn. Annual litterfall biomass flux (Mean ± SD = 3.3 ± 0.5 *vs* 2.0 ± 0.5 Mg ha^{-1}) and N return (34.8 ± 16 *vs* 9.1 ± 2.8 kg N ha^{-1}) were higher in the MBF than in the CF. At the ecosystem level, litterfall C/N was lower in the MBF (mean C/N ratio = 60.1 ± 15, $n = 3$ years) suggesting decreased N use efficiency compared with CF (mean C/N ratio = 103 ± 19.6, $n = 3$ years). At the species level, subordinated (subcanopy) tree species in the MBF had significantly lower C/N ratios (<50) of litterfall than the dominant trees in the CF and MBF (>85). The litterfall C/N ratio and percentage N retranslocated were significantly correlated and were lower in the MBF. The higher net N mineralization in soils of the MBF is related to a lower N use efficiency at the ecosystem and species level.

Key words: Chiloé National Park, *Fitzroya cupressoides*, litterfall C/ N ratio, N retranslocation, *Nothofagus nitida*, southern temperate forests.

INTRODUCTION

Because of their remote location, high-latitude forests in southern South America receive one of the lowest atmospheric inputs of inorganic nitrogen (N) in the world (Galloway *et al.* 1996; Weathers & Likens 1997; Weathers *et al.* 2000). Consequently, internal cycling of N becomes the primary source of inorganic N for forest productivity. Two internal fluxes of N are of primary importance for plant growth and the efficient use of available N. First, the release of N temporarily immobilized in plant litter and dead microbial biomass via microbial mineralization, and second, the retrieval of N from senescent leaves to perennial tissues to be re-utilized by plants in the next growing season (Chapin & Kedrowski 1983; Killingbeck 1986). Therefore, we define highly efficient ecosystems as those that are composed of species that are able to recycle (reuse) and/or retain a higher proportion of the nutrients that circulate within the ecosystem and therefore are largely independent of external N inputs.

Mineralization of N contained in dead organic matter, while providing energy for microbial metabolism, makes inorganic N available for plant uptake. The proportion of N that becomes available for plant growth depends on the ratio of total N to total carbon (C) in the mineralized substrate (Rosswall 1982). In forest ecosystems, C/N ratios of litter affect soil processes, such as the rates of decomposition and net N mineralization of organic matter and the availability of nutrients in soil (Scott & Binkley 1997; Fassnacht & Gower 1999; Ferrari 1999). We propose that, in unpolluted regions of the world such as southern Chile, physiological traits of trees that determine N use efficiency (NUE) such as litterfall C/N ratios, are key regulators of ecosystem N production in soil. The nutrient use efficiency of litter production in an ecosystem is a collective property of the species assemblage in that ecosystem. In N-limited ecosystems and particularly those composed of long-lived perennials,

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*Corresponding author. †Correspondence address.

Accepted for publication May 2003.

such as forests, species tend to reallocate a higher proportion of leaf N to perennial tissues before leaf fall, thus making a more efficient use of N (Chapin 1980; Vitousek 1982). However, more recent studies show that the nutrient status of leaves and site productivity are not associated with nutrient resorption efficiency (e.g. percentage retranslocation), because of environmental constraints such as water availability in soil (Aerts 1996; Knops *et al.* 1997). Therefore, complementary NUE indices of species should be used. Highly efficient species should have a higher C/N ratio in litterfall, because they lose a lesser amount of N in relation to the amount of carbon fixed (Chapin 1980; Vitousek 1982, 1984). Another index proposed is the N concentration in senesced leaves (resorption proficiency; Killingbeck 1996).

For woody species of southern temperate forests, leaf C/N ratio, as an NUE index, may be associated with other ecophysiological traits such as the degree of sclerophylly (fibre to protein ratio in leaves), phosphorous concentration, and the Ca/K ratio of leaves (Weinberger *et al.* 1973; Pérez 1994). Some of these characteristics may supply an alternative explanation for differences in C/N ratios among species.

In the present paper, we document the dynamics of fine litterfall and discuss NUE in two old-growth forest ecosystems in southern South America, applying different and complementary NUE indices proposed in the literature. We compared NUE in two coastal montane forests: (i) a conifer forest and (ii) a broadleaf, evergreen angiosperm forest. The two forests grow in a similar climate and on the same soil type on Chiloé Island, southern Chile (Pérez *et al.* 1998; Zarin *et al.* 1998). The comparison is interesting because, despite the similarities in site conditions, these forests differ greatly in canopy composition, structure and dynamics (Armesto *et al.* 1995; Pérez *et al.* 1998). Our main hypothesis is that differences in litterfall patterns and NUE between these two unpolluted, old-growth forests should be coupled to structural characteristics and dynamics of canopy trees that affect the internal N cycle in each forest. Specifically, and consistent with the hypothesized positive feedback mechanism that controls the N cycle, we predict that conifer forests, with a slower net rate of N mineralization in soil, should be more efficient in their N use than broadleaf evergreen angiosperm forests, with a faster net N mineralization rate (Pérez *et al.* 1998).

The main questions addressed here were: (i) do conifer and angiosperm forests differ in litterfall dynamics and NUE?; (ii) how do litterfall dynamics and NUE relate to the internal N cycle in each forest?; and (iii) how do litterfall dynamics and NUE in southern temperate forests compare with other evergreen forests of the world? Our main objective was to estimate and compare NUE, at both the ecosystem and species level, by comparing C/N ratios and percentage N of fine litterfall, and N retrieval from leaf tissues before leaf fall.

METHODS

Study sites and forest types

The study was conducted in two montane primary coastal forests (550–680 m a.s.l.) located in Chiloé National Park, Chiloé Island (42°30′S), Chile. Forests in the study area are all evergreen and dominated by a mixture of broad-leaved and conifer trees (Armesto *et al.* 1995; Pérez *et al.* 1998). We studied two forest types: (i) a conifer-dominated forest (CF), where the long-lived Cupressaceae *Fitzroya cupressoides* was the main canopy species; and (ii) a mixed broad-leaf angiosperm forest (MBF) with a canopy dominated by the Fagaceae *Nothofagus nitida*, but including shade-tolerant conifers such as *Podocarpus nubigena* (Podocarpaceae) and fast-growing angiosperms such as *Drimys winteri* (Winteraceae). The MBF is representative of the North Patagonian forest type, as described by Veblen *et al.* (1983), which is distributed from 40 to 47°S in southern Chile. North Patagonian rainforests are composed of species of contrasting biogeographical origins, including Australasian, Neotropical and endemic species (Villagrán & Hinojosa 1997). According to palynological records, species of *Nothofagus, Fitzroya* and *Podocarpus* persisted on Chiloé island during the last glacial maximum (20 000–23 000 years ago), occupying lowland sites that remained unglaciated (Villagrán *et al.* 1996). Conifer forests dominated by *Fitzroya cupressoides* occur in discrete patches at high elevations (>600 m a.s.l.) and MBF at slightly lower elevations (500–600 m a.s.l.) in the coastal range between 40 and 43°S. These two forest types differ greatly in regeneration dynamics and major disturbance regimes, with a faster canopy turnover of <300 years, associated with frequent gap-phase dynamics, for MBF, and a slower canopy turnover of >600 years, associated with infrequent large-scale catastrophic events, for CF (Armesto *et al.* 1995). Forest fires are an important factor of forest disturbance in CF, whereas wind blow-downs are frequent in MBF (Lusk 1996). A previous study showed that soil C/N ratios were lower (33.4 *vs* 39.0) and net N mineralization rates in soils were higher (37 *vs* 23 kg ha^{-1} $year^{-1}$) in the MBF compared with the CF (Pérez *et al.* 1998).

The prevailing climate in the study area is wet-temperate with a strong oceanic influence and an annual precipitation of 5000–6000 mm, as estimated from 5-year records taken at approximately 650 m a.s.l. in the study site. The mean summer temperature is 10.2°C and the mean winter temperature is 6.2°C. Seasonal temperature fluctuations in these rainforests are reduced by the strong oceanic influence, but the summer months (December–March) tend to be drier than the rest of the year (20% of the total annual rainfall), giving a slight Mediterranean character to the climate (Arroyo *et al.* 1996). Microclimatic records of solar radiation, air and soil temperature indicate slight differences between the forests, with lower minimum air and soil temperatures in the CF. This forest type is mostly distributed on north-west slopes that are exposed to the wind, whereas the MBF is more frequently distributed on south and south-west sheltered slopes and at lower elevations. Disturbance regimes, together with slope aspect heterogeneity and topography may explain the mosaic of forest types in the landscape (Armesto *et al.* 1995; Pérez *et al.* 1998). Soils are predominantly cambisols with a pH ranging from 4 to 5 and a high content of organic matter (50% total carbon; Pérez *et al.* 1998; Zarin *et al.* 1998). Both forests grow on the same geological substrate of Palaeozoic michaschists.

In the CF, *Fitzroya cupressoides* accounts for 56% of the total basal area, whereas three other tree species, *Pilgerodendron uviferum* (Cupressaceae, 15%), *Tepualia stipularis* (Myrtaceae, 14%) and *Nothofagus nitida* (11%) account for most of the remainder. Coring of canopy trees has indicated a minimum stand age of 400–500 years for the CF. The stand developed slowly, following a large-scale disturbance, with little or no regeneration of *F. cupressoides*. In contrast, the MBF is characterized by a faster canopy turnover, as documented by the frequent tree-fall gaps and the abundant regeneration of canopy trees (Armesto *et al.* 1995). *Nothofagus nitida* and *Drimys winteri* together account for 72% of the basal area. Other canopy species are *Laureliopsis philippiana* (Monimiaceae, 12%) and the conifer *Podocarpus nubigena* (6%). A well-developed subcanopy is dominated by *Amomyrtus luma* (Myrtaceae, 3%), and the bamboo *Chusquea* sp. Coring of canopy trees has indicated that the oldest trees in this stand are 200–250 years old. More detailed descriptions of forest structure and dynamics are given by Armesto *et al.* (1995) and Pérez *et al.* (1998).

Litterfall biomass and N flux

Between May 1995 and March 1999, fine litter material was retrieved monthly from 16 collectors in the CF and 12–16 collectors in the MBF. Collectors were placed regularly every 10 m along transect lines running from the top to the bottom of the slope covering ~0.1 ha in each forest. Each collector consisted of a 0.5-m diameter metal ring holding a plastic net funnel (1 mm mesh size) positioned 1 m above the ground. Fine litter material from each collector, consisting predominantly of leaves, twigs and branches (<1 cm diameter), and occasionally of flowers, epiphytes, seeds and insect remains, was taken separately to the laboratory to determine its dry weight. Monthly inputs of fine litter biomass were expressed as g dry mass per m^2 of trap. From January 1996 to March 1999, samples of three randomly selected traps from each forest were ground separately and analysed for total C and N concentrations by flash combustion in a Carlo Erba Element Analyser (NA 2500) at the Universidad de Chile. N fluxes associated with fine litterfall were obtained by multiplying the concentration of total N in litter samples by the biomass input for each month. Although leaching of nutrients and C, and decomposition of biomass, may have occurred as the litter sat inside the collectors for 1 month before processing, these processes were assumed to be identical for all species and collectors. Consequently, comparisons between forests are valid, although absolute values may be slightly overestimated because of leaching.

In addition, selected litter samples ($n = 8$ in the CF and $n = 4$–7 in the MBF) for the months of January (summer), April (autumn), July (winter) and October (spring) 1996 were sorted by species and the dry weight ascertained for each specific type of litter. Collected material consisted of 24–95% leaves, and the remainder was twigs (<1 cm diameter), seeds, flowers, epiphytes and insect remains. Samples of each species that contributed >1% to total litter dry mass, were ground for determination of total N and C concentrations as described above.

NUE indices

In each forest, fresh leaves of all trees represented in litterfall were taken from hand reachable branches ($n = 3$ trees per species) in August and October 1999. N concentration in fresh leaves obtained by this method did not differ significantly from the results obtained at the study site by Vann *et al.* (2002), who collected fresh leaves at different levels of the tree canopy. Samples were dried, ground and analysed for total C and N concentrations using the same methodology described for litter material. For each species we calculated an average index of internal retranslocation, which was estimated as the difference between foliar N concentration and litterfall N concentration (Chapin 1980; Vitousek & Sanford 1986; Veneklaas 1991). The percentage of N retranslocated (%RT) was calculated as:

$$\%\,RT = (\%N_{leaves} - \%N_{litterfall})/\%N_{leaves} \times 100.$$

%RT is a direct estimate of species NUE, that is, a high %RT coincides with a high NUE (Vitousek 1982). Mean retranslocation values for each species were the averages of all seasonal values.

Considering environmental constraints on %RT (Killingbeck 1996), we used two additional indices to estimate NUE. First, following Vitousek's (1982) definition of nutrient use efficiency as the amount of organic matter lost (in litterfall or root turnover) or stored (biomass increment) per unit of nutrient lost or stored, we used C/N ratios of litterfall for each species and for all species pooled (ecosystem level) as indicators of NUE at the species and ecosystem level, respectively. This second index implicitly relates NUE and productivity (Berendse & Aerts 1987) because it refers to the amount of fixed C. Finally, we used the concentration of N in litter (%) as an index of resorption proficiency at the species level. This index estimates the absolute level to which nutrients are reduced in senescing leaves (Killingbeck 1996). Values less than 0.7% indicate a high resorption proficiency (Killingbeck 1996).

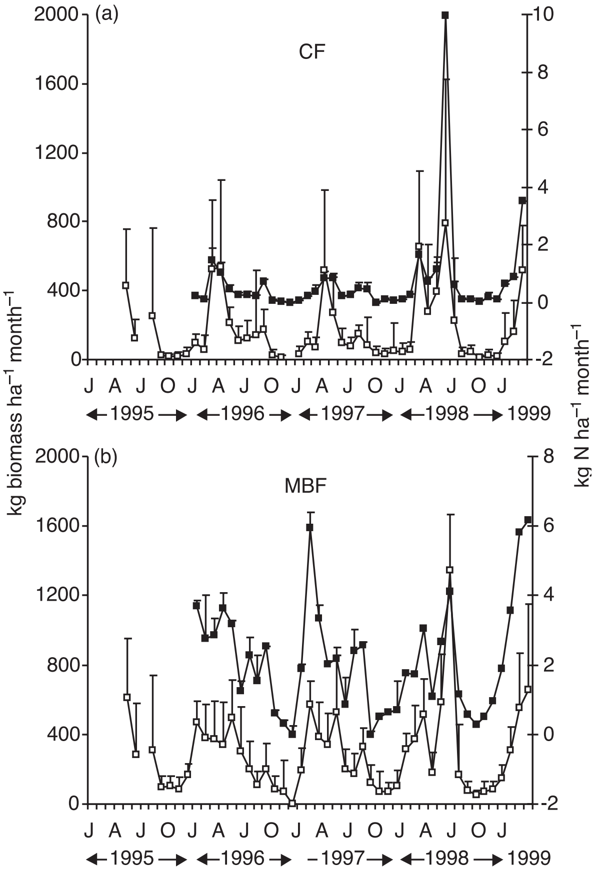

Fig. 1. (a) (□) Litterfall biomass and (■) nitrogen flux in litterfall over 3 years in a conifer forest (CF) dominated by *Fitzroya cupressoides* in Chiloé National Park, southern Chile. Bars represent ±SE, for $n = 12–16$ litter collectors for biomass flux and $n = 2–3$ for N flux. (b) (□) Litterfall biomass and (■) nitrogen flux in litterfall over three years in a mixed broad-leaf forest (MBF) dominated by *Nothofagus nitida* and *Drimys winteri* in Chiloé National Park, southern Chile. Bars represent ±SE, for $n = 12–16$ litter collectors for biomass flux and $n = 2–3$ for N flux. Gaps represent missing data. J, January; A, April; J, July; O, October.

Net N mineralization

We randomly selected three individuals of *Fitzroya cupressoides* in the CF, and two of *Nothofagus nitida* and one of *Podocarpus nubigena* in the MBF. In the soil surrounding the base of each tree, we set up one circular plot of 3-m radius. Monthly, from April 1997 until March 1999, we collected six soil samples (0–10 cm, A_h horizon) around the perimeter of each plot. Soil samples were sieved (to remove roots) and homogenized in the field. One subsample per plot was taken to the laboratory for analysis of the initial ammonium and nitrate contents, and a second subsample was placed inside a polyethylene bag, returned to the soil in the same place, and incubated for 1 month. After 30 days, incubated samples were removed and taken to the lab for the final analysis of available N (nitrate-N + ammonium-N) by fractionated steam distillation. Net N mineralization was estimated as the difference between initial and final inorganic N contents of incubated soil samples (Pérez *et al.* 1998).

Statistical analyses

We used a one-way, repeated measures ANOVA (Zar 1996) to evaluate the statistical significance of forest type on the dependent variables: litterfall biomass, litter N flux, and C/N ratios of fine litterfall, in monthly collected samples over 3 consecutive years. We used a one-way ANOVA to assess significant differences in litterfall C/N ratios and %N among tree species, followed by an a posteriori Tukey's test (Systat, 1996). We used one-way ANOVA (Systat, 1996) to evaluate the effect of forest type on monthly rates of net N mineralization ($n = 23$). Pearson's partial correlation analyses were used to estimate the degree of association between the NUE indices, C/N ratio and %N in litterfall and %RT, % N and C/N ratios of fresh leaves.

RESULTS

Litterfall biomass and N fluxes

Ecosystem-level comparisons

Fine litter production in both evergreen forests (Fig. 1) was continuous throughout the year, but there were pulses of higher litterfall in early mid-autumn (April–May) and a marked decrease in litter flux in both forests during spring (September–December) each year. The autumn pulses were more pronounced in the CF (Fig. 1a) than in the MBF (Fig. 1b). The higher fluxes of fine litter recorded in June 1998 in both forests were strongly influenced by a severe winter storm. Repeated measures ANOVA showed significant effects of forest type, year and month on litterfall biomass input (Table 1). Annual litterfall was significantly higher in the MBF (mean ± SE = 3.33 ± 0.53 Mg ha^{-1} $year^{-1}$, $n = 3$) than in the CF (2.04 ± 0.49 Mg ha^{-1} $year^{-1}$), and this difference was maintained in all years of the study.

The N flux to the forest floor through litterfall followed a similar trend to biomass over the 3 years of the study (Fig. 1). The two variables were strongly correlated in each forest (Pearson's $r = 0.73$, $P < 0.001$, $n = 38$ in each forest) but there was a higher variation in the N input to the forest floor in the MBF than in the CF. The repeated measures ANOVA revealed significant effects of forest type and month on total litterfall N flux (Table 2). There was no effect of year. The N flux in litter was almost four times higher in the MBF (mean ± SE = 34.8 ± 16 kg N ha^{-1} $year^{-1}$, $n = 3$) than in the CF (9.1 ± 2.8 kg N ha^{-1} $year^{-1}$, $n = 3$).

Species-level comparisons

There was a strong correlation between each species' basal area and their estimated fine litter inputs in the CF (Pearson's $r = 0.97$, $P < 0.006$, $n = 5$), but not significant correlation in the MBF ($r = 0.85$, $P = 0.07$, $n = 5$). The dominant canopy tree in the CF, the conifer *Fitzroya cupressoides*, made the greatest contribution to fine litterfall biomass (up to 64%) and to N return (up to 69%) to the forest floor (Table 3). Two subordinate tree species in CF, *Tepualia stipularis* and *Pilgerodendron uviferum*, and the understorey species *Podocarpus nubigena*, which was represented only by juveniles, made smaller contributions (up to 2.5% individually) to stand litterfall.

The higher litterfall biomass and N return to the forest floor documented in the MBF was due to its two dominant canopy species, the angiosperms *Drimys winteri* and *Nothofagus nitida*, which contributed together 83% of the total annual litterfall (Table 3). Smaller contributions (up to 9% individually) were made by the subordinate species *Laureliopsis philippiana* and *Podocarpus nubigena*, and by the subcanopy tree *Amomyrtus luma*.

C/N ratios and NUE

Ecosystem-level comparisons

Repeated measures ANOVA showed significant effects of forest type, year and month on C/N ratios of litterfall (all species pooled; Table 4). C/N ratios (all species pooled) were significantly higher in the CF (mean ± SE = 103 ± 19.6, $n = 3$) than in the MBF (60.1 ± 15), indicating that species in the CF had a higher NUE. In both forests, litterfall C/N ratios almost doubled from summer to autumn each year, reaching a maximum in April, and decreased again towards the end of winter and early spring (Fig. 2).

Species-level comparisons

Fitzroya cupressoides, the dominant tree in the CF, had the highest C/N ratio of litterfall (>100) among all species compared (Table 3), with the maximum %RT and one of the lowest proficiency values (0.55%), indicating a high NUE. The main canopy species in the MBF, *Drimys winteri* and *Nothofagus nitida*, both had lower litter C/N ratios than the dominant tree species in CF (Table 3), but differences between forests were

Table 1. Repeated measures ANOVA for biomass input of fine litter to the forest floor

Source of variation	d.f.	*F*	*P*
Between subjects			
Forest	1	34.912	<0.0001
Error	12		
Within subjects			
Year	2	9.607	0.001
Year × Forest	2	3.038	0.067
Error	24		
Month	11	61.57	<0.0001
Month × Forest	11	15.792	<0.0001
Error	132		
Year × Month	22	24.54	<0.0001
Year × Month × Forest	22	12.092	<0.0001
Error	264		

Table 2. Repeated measures ANOVA for N input in fine litter to the forest floor

Source of variation	d.f.	*F*	*P*
Between subjects			
Forest	1	16.703	<0.015
Error	4		
Within subjects			
Year	2	0.515	0.616
Year × Forest	2	3.73	0.087
Error	8		
Month	11	2.99	0.005
Month × Forest	11	1.853	0.073
Error	44		
Year × Month	22	2.78	<0.0001
Year × Month × Forest	22	0.801	0.716
Error	88		

Table 3. Per cent basal area (BA%), average biomass flux (kg ha^{-1} month^{-1}), nitrogen flux (kg N ha^{-1} month^{-1}) to forest floor, C/N ratios of litterfall and fresh leaves, N concentration (%) in fresh and litterfall leaves and percentage retranslocated N (%RT) from fresh leaves, for the dominant (>30%) and subordinate (<30% BA) tree species in two old-growth temperate forests (CF and MBF) in Chiloé National Park, southern Chile

	BA (%)	Biomass flux (kg ha^{-1} month^{-1})	N-flux (kg N ha^{-1} month^{-1})	C/N litter	C/N leaves	% N leaves	%N litter	RT (%)
Conifer forest (CF)								
Dominant species								
Fitzroya cupressoides	55.9	105 ± 89	0.53 ± 0.45	113.4 ± 6.7^{ac}	63.8 ± 17.3	0.87 ± 0.12	0.55 ± 0.04^{a}	37.1
Subordinate species								
Tepualia stipularis	13.9	23 ± 10	0.10 ± 0.04	99.2 ± 8.8^{c}	66.7 ± 8.9	0.78 ± 0.05	0.50 ± 0.04^{a}	35.7
Nothofagus nitida	11.0	10 ± 6	0.07 ± 0.03	85.8 ± 12.9^{ac}	NA	NA	0.67 ± 0.1^{ab}	NA
Pilgerodendron uviferum	15.4	5 ± 2	0.04 ± 0.02	76.4 ± 6.8^{abcd}	46.8 ± 4.0	1.12 ± 0.04	0.73 ± 0.05^{abd}	34.7
Podocarpus nubigena	1.7	4 ± 1	0.03 ± 0.01	82.3 ± 10.2^{abcd}	NA	NA	0.66 ± 0.1^{ab}	NA
Mixed broad-leaved forest (MBF)								
Dominant species								
Drimys winteri	30.2	86 ± 35	0.68 ± 0.24	72.1 ± 5.8^{abd}	52.1 ± 2.1	0.97 ± 0.02	0.87 ± 0.07^{abd}	10.3
Nothofagus nitida	41.7	56 ± 17	0.40 ± 0.03	64.2 ± 8.6^{abd}	48.2 ± 2.8	1.07 ± 0.03	0.79 ± 0.09^{abd}	26.3
Subordinate species								
Podocarpus nubigena	6.0	8 ± 5	0.08 ± 0.01	48.4 ± 5.5^{bd}	43.8 ± 1.1	1.13 ± 0.01	1.14 ± 0.1^{de}	0.0
Amomyrtus luma	2.6	4 ± 1	0.04 ± 0.01	48.1 ± 2.5^{bd}	43.1 ± 2.5	1.14 ± 0.04	1.06 ± 0.05^{bde}	6.4
Laureliopsis philipiana	11.7	16 ± 9	0.20 ± 0.06	41.1 ± 5.3^{d}	28.4 ± 1.3	1.67 ± 0.04	1.41 ± 0.25^{e}	15.5

Data are the average (±SE) of season means for year 1996 ($n = 4$ for litter values, $n = 2$ for leaf values). Different superscripts represent statistically significant differences among species in litterfall C/N ratios and %N (Tukey's post-hoc test, $P < 0.05$). NA, Data unavailable.

largely derived from the fact that the lowest C/N ratios (<50) among all species compared were associated with the litterfall of *Laureliopsis philippiana, Podocarpus nubigena*, and *Amomyrtus luma* in the MBF (Table 3). *Amomyrtus luma* and *Podocarpus nubigena* also had the lowest %RT (6.4 and 0%, respectively; Table 3). All the species in MBF had values of resorption proficiency (%N litter) of greater than 0.7%, indicating a low NUE (Table 3).

Tree species that were present in both forests, such as *Nothofagus nitida* and *Podocarpus nubigena*, allowed us to identify a trend towards lower litterfall C/N ratios in the MBF (Table 3), reflecting the differences in the below-ground N cycle between sites.

Correlations among NUE indices

The C/N ratio of litterfall and %RT were significantly and positively correlated (Table 5). In addition, %RT was significantly correlated with resorption proficiency (%N in litter). The C/N ratio of litterfall was negatively correlated with %N in fresh leaves and positively correlated with leaf C/N ratio.

Net N flux from mineralization

The net rates of N production measured in field incubations were generally negative, indicating strong immobilization. Adding positive monthly values of net N mineralization, we estimated the average net flux of mineralized N in the CF to be 2.44 ± 1.7 kg N ha^{-1} year^{-1} (mean ± SE, $n = 2$ years) and in the MBF to be 1.22 ± 1.00 kg N ha^{-1} year^{-1}. Over the 23 months of field incubation, the net N mineralization rates did not differ significantly between the two forests compared (one-way ANOVA, $F = 0.17$, d.f. = 1, $P = 0.68$).

Table 4. Repeated measures ANOVA for C/N in litterfall to forest floor

Source of variation	d.f.	*F*	*P*
Between subjects			
Forest	1	104.722	0.001
Error	4		
Within subjects			
Year	2	29.137	<0.0001
Year × Forest	2	57.687	<0.0001
Error	8		
Month	11	28.443	<0.0001
Month × Forest	11	2.602	0.012
Error	44		
Year × Month	22	4.198	<0.0001
Year × Month × Forest	22	1.875	0.021
Error	88		

DISCUSSION

Ecosystem and species NUE in conifer and angiosperm forests

At the ecosystem level, the CF is characterized by a higher NUE than the MBF, as indicated by the significantly higher C/N ratios of litterfall in the former. This conclusion is consistent with the general view that conifer-dominated forests are more N use efficient than angiosperm-dominated forests (Vitousek 1982; Yin 1994), even though in the present study both forests were composed entirely of evergreen tree species,

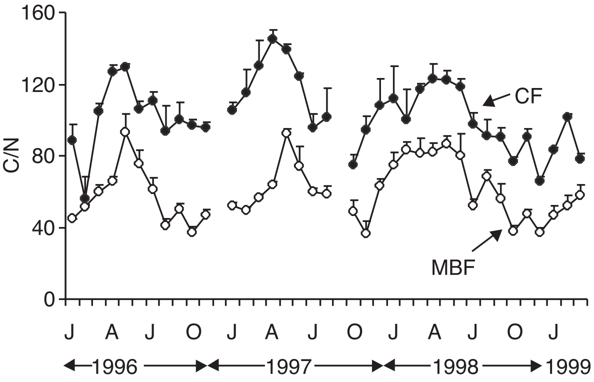

Fig. 2. Monthly variability of C/N ratios of litterfall (all species pooled) over three subsequent years in (●) a conifer forest (CF) and (○) a mixed broad leaf forest (MBF) in Chiloé National Park, southern Chile. Bars represent ±SE, for $n = 3$ litter collectors per month. Gaps represent missing data. J, January; A, April; J, July; O, October.

Table 5. Pearson correlations matrix between N use efficiency indices (litterfall C/N, %RT and litterfall %N) and leaf %N and C/N ratio ($n = 10$ samples)

	C/N$_{\text{litterfall}}$	%RT	%N$_{\text{leaf}}$	C/N$_{\text{leaf}}$	%N$_{\text{litterfall}}$
C/N$_{\text{litterfall}}$	1.000				
% RT	0.801*	1.000			
%N$_{\text{leaf}}$	−0.777*	−0.412	1.000		
C/N$_{\text{leaf}}$	0.914**	0.597	−0.951***	1.000	
%N$_{\text{litterfall}}$	−0.903**	−0.780*	0.881**	−0.923**	1.000

Significance level: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 6. Annual internal ecosystem fluxes of litter biomass (Mg ha^{-1}) and nitrogen (kg N ha^{-1}) associated with litterfall for selected evergreen, angiosperm and conifer-dominated, forests of the world reported in the literature

Forest type	Location	Biomass flux (Mg ha^{-1} $year^{-1}$)	N flux (kg N ha^{-1} $year^{-1}$)	Reference
Temperate				
Conifer forest (*Fitzroya cupressoides*)	Chile	2 ± 0.5	9.1 ± 2.8	This study
Pacific Silver Fir	Washington, USA	2.7	10.6	Johnson & Lindberg 1992
Red spruce (*n* = 2)	North Carolina, USA	1.8 ± 0.1	12.1 ± 1.3	Johnson & Lindberg 1992
Douglas Fir	Washington, USA	1.8	14.8	Johnson & Lindberg 1992
Loblolly Pine (*n* = 2)	Tennessee, USA	3.1 ± 0.6	16.6 ± 4.0	Johnson & Lindberg 1992
Mixed broad-leafed forest (*Nothofagus nitida*)	Chile	3.3 ± 0.5	34.8 ± 1.6	This study
Lowland mixed forest	New Zealand	7.8	–	Enright 1999
Tropical				
Montane tropical rainforest	Colombia	4.3	34.2	Veneklass 1991
Montane tropical rainforest (*n* = 9)	Palaeo- and Neotropics	6.4 ± 2.0	64.0 ± 25.0	Vitousek & Sanford 1986
Lowland tropical rainforest (*n* = 2)	Venezuela	7.2 ± 0.6	62.5 ± 4.9	Coomes 1997
Lowland evergreen subtropical	Australia	6.2	–	Hegarty 1991

Means (±SD) are indicated when available.

whereas previous work compared conifer-dominated with deciduous angiosperm forests.

Fluxes of biomass and N associated with leaf-fall are important components of the internal N cycle of a forest ecosystem. These fluxes are determined largely by the ecophysiological and anatomical characters of the main tree species in the forest canopy (Reich *et al.* 1992; Aerts 1996). As expected, tree species with a larger basal area in each forest contributed more to litterfall biomass, and N flux to the forest floor (Table 3). Consequently, the magnitudes of these internal fluxes were explained to a large extent by the dominant canopy species and to a much lesser extent by subordinate or subcanopy species.

In the present paper, we compared different and complementary NUE indices. The statistical correlations (Table 5) found between %RT and C/N ratios of litterfall and between %RT and %N in litter showed that these three indices were good estimators of NUE at the species level and that they could be used independently. Moreover, these positive correlations suggested a biochemical basis for Killinbeck's N proficiency (%N), in other words, %N in litterfall was accounted for mainly by percentage resorption before leaf-fall (Table 5). Also, the negative correlation between %N in green leaves and C/N ratios of litterfall indicated that those species having a higher leaf N concentration are less N use efficient, as in the case of all subordinate species in the MBF (Table 3). However, the significant positive correlations found between litterfall C/N ratio and %N, and between leaf C/N ratio and %N may have resulted from a mathematical artifact (Knops *et al.* 1997). In addition, the positive correlation between litterfall C/N ratio and green leaf C/N ratio showed that those species with a greater amount of carbon per unit of N in their leaves were also capable of retaining more N per unit carbon lost in litterfall. Examples of the latter case were the dominant tree species in the CF, *Fitzroya cupressoides*, and the subordinate species in the CF, *Tepualia stipularis*. The values of %RT found in this paper (<40%) are in the lower range reported for evergreen trees and shrubs (Aerts 1996). Differences in C/N ratios of litterfall between the dominant species in the CF and MBF were rather small (Table 3). However, there were pronounced differences in litter C/N ratios, %RT and resorption proficiency among subordinate and subcanopy species in each forest.

Internal N cycle and NUE

Compared with data reported for the sampling period 1994–1996 (Pérez *et al.* 1998), there was a strong reduction in net N mineralization rates in soils both in the MBF and CF during the period 1997–1999. However, significant differences in litterfall dynamics were maintained. Combining annual rates of net N mineralization obtained for the years 1994–1996 (Pérez *et al.* 1998) and the data obtained in the present study for the period 1997–1999 gives a 4-year average of 11.9 ± 2.8 kg N ha^{-1} $year^{-1}$ in the CF and 17.8 ± 4.8 kg N ha^{-1} $year^{-1}$ in the MBF. These figures were consistent with an overall trend of slower net N mineralization in the CF, suggesting that a higher ecosystem NUE in old-growth, conifer-dominated forests may be a direct consequence of their slower N flux from mineralization. Accordingly, we took these data as evidence of a positive feedback mechanism controlling the internal N cycle in these forest ecosystems, as suggested by Gosz 1981) and Vitousek (1982) for other temperate and tropical forests. According to this hypothesis, lower N flux from litter and higher litterfall C/N ratios should slow down N mineralization in soil, leading to a more efficient internal N cycle.

Patterns of litterfall and internal N flux in comparison to other forests

Chilean temperate forests, confined to the western margin of southern South America, occur in a strongly oceanic, non-seasonal climate (Alaback 1991; Arroyo *et al.* 1996) and therefore litter flux is less synchronous and has a much less pronounced seasonality than in European or North American deciduous forests at similar latitudes. Patterns of leaf-fall in forests may be affected by a number of environmental factors, including windstorms, seasonal droughts during summer and by the shortening of day-length during autumn (Cuevas & Medina 1986; Proctor *et al.* 1989; Williams & Tolome 1996; Enright 1999). In the present study we documented a greater seasonality of leaf-fall in the CF than in the MBF (Fig. 1), with most extensive litterfall between March and May in both forests. However, a combination of environmental factors, such as those mentioned above, produced a continuous flux of litter throughout the year. Weak seasonal trends were also detected for litterfall C/N ratios in both forests, with peaks during autumn. We did not find other studies reporting seasonal C/N ratios of litterfall for comparison. Annual N fluxes associated with litterfall at CF were lower than values reported for equivalent, conifer-dominated, North American temperate forests (Table 6). Among angiosperm-dominated, evergreen forests (either tropical or temperate), MBF also had one of the lowest values of annual litterfall N flux (Table 6). Relatively lower values of N return associated with litter in Chiloé forests could be expected on the basis of the extremely slow N cycle (net N mineralization <20 kg ha^{-1} $year^{-1}$) and strong N limitation (hydrological outputs of inorganic N <1 kg ha^{-1} $year^{-1}$), as documented for these evergreen forests in previous studies (Hedin *et al.* 1995; Pérez *et al.* 1998; Perakis & Hedin 2001, 2002). Turnover rates of canopy foliage for MBF and CF were also extremely slow and were estimated as approximately 5 and 15 years, respectively (Vann *et al.* 2002). These lines of evidence suggest a tight internal and very efficient N cycle for these two remote southern temperate forests, compared with other forests of the world.

ACKNOWLEDGEMENTS

The research was funded by the A. W. Mellon Foundation, by a Presidential Chair in Sciences to J. J Armesto, and by Fondecyt 1990946. Final manuscript preparation was supported by Millennium Nucleus grant P99-103-F ICM, IAI-CRN-012 and Fondecyt-Fondap Grant 1501–0001 to the Center for Advanced Studies in Ecology and Biodiversity. We thank J. Ríos, J. Nonque and CONAF-X Region, for logistic support; L. Cavieres, O. Jorquera, B. Baker, L. Portnoff and P. MacPherson for field assistance, and C. Lusk and two anonymous referees for comments. This is a contribution from CPES and from the Research Program of Estación Biológica 'Senda Darwin', Ancud, Chile.

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