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RESEARCH ARTICLE

Litterfall, litter decomposition and nitrogen mineralization in old-growth evergreen and secondary deciduous *Nothofagus* forests in south-central Chile

Aporte, descomposición de hojarasca y mineralización de nitrógeno en bosques siempreverdes de antiguo crecimiento y bosques secundarios deciduos, centro-sur de Chile

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ABSTRACT

South Chilean forest ecosystems represent one of the largest areas of old-growth temperate rainforests remaining in the Southern hemisphere and have a high ecological value, but suffer from deforestation, invasion by exotic species, fragmentation, and increasing atmospheric nitrogen (N) deposition. To support sustainable forest management, more knowledge is required on nutrient cycling of these ecosystems. Therefore, a descriptive study of nutrient dynamics was done in four Valdivian rainforests in the lower Andes range of south Chile: old-growth and altered evergreen stands and unmanaged and managed secondary deciduous stands. Time series were measured for (i) mass (four year) and nutrient content (N, K, Ca, and Mg; one year) of litterfall, (ii) decomposition and nutrient dynamics (N, C, K, Ca, Mg, and P; one year) of leaf litter and *Saxegothaea conspicua* bark litter, and (iii) in situ topsoil net N mineralization (one year). Litterfall in the four stands ranged from 3.5 to 5.8 ton ha^{-1} yr^{-1}, was temporarily lower in the managed than in the unmanaged deciduous stand and had a different seasonality in the evergreen stands than in the deciduous stands. Leaf litter decomposed faster (on average 32 % mass loss after one year) than bark litter (8 %) but without significant differences between leaf litter types. Net N in evergreen leaf litter decreased during decomposition but increased in deciduous leaf litter. Net soil N mineralization was fastest in the pristine evergreen stand, intermediate in the deciduous stands and slowest in the altered evergreen forest. Given the absence of replicated stands, the definite impact of forest type or management regime on the internal nutrient cycling cannot be demonstrated. Nevertheless, the results suggest that management can affect nutrient turnover by altering species composition and forest structure, while recent (five years) selective logging in secondary deciduous forest did not affect litter decomposition or N mineralization rates in the present study.

Key words: Andisol, Chile, nitrogen cycling, nutrient dynamics, temperate rainforest.

RESUMEN

Los ecosistemas forestales del sur de Chile presentan un gran valor ecológico pues constituyen una de las mayores áreas del hemisferio Sur con existencias de bosques templados lluviosos. Están sometidos a procesos de deforestación, invasión de especies exóticas, fragmentación e incremento de depositación de nitrógeno (N) atmosférico. Para apoyar su manejo sustentable se requiere de mayor conocimiento en el ciclo de nutrientes de estos ecosistemas. Se estudia la dinámica de nutrientes en cuatro sitios de bosques lluviosos valdivianos de la precordillera de los Andes, centro-sur de Chile: un bosque siempreverde de antiguo crecimiento prístino y otro alterado, un bosque caducifolio secundario con manejo silvícola y otro sin. Durante el período octubre 2002 - septiembre 2006, se estimaron (i) masa de la hojarasca (cuatro años) y contenido de nutrientes de la hojarasca (un año), (ii) descomposición y dinámica de nutrientes de hojarasca (un año) y de la corteza de *Saxegothaea conspicua*, y (iii) mineralización neta de nitrógeno (N-min) en el suelo in situ (un año). El aporte de hojarasca en los cuatro sitios fluctúa desde 3.5 hasta 5.8 ton ha^{-1} $año^{-1}$, y es temporalmente menor en bosque caducifolio manejado, respecto del caducifolio sin manejo. Además, presentan una estacionalidad en los siempreverdes que es diferente, respecto de los deciduos. La hojarasca se descompone más rápidamente (promedio 32 % pérdida de masa después de un año) que la corteza (8 %), pero no se presentaron diferencias significativas en la hojarasca. El N neto en la hojarasca de los bosques siempreverdes disminuye durante la descomposición, pero se incrementa en la hojarasca de los deciduos. La N-mineralización neta del suelo fue completa en el bosque siempreverde prístino, intermedia en los bosques deciduos y el más baja en el bosque siempreverde alterado. Dada la ausencia de réplicas en las parcelas, no puede ser demostrado el impacto definido del tipo de bosque o régimen de manejo en el ciclo interno de nutrientes. Sin embargo, los resultados sugieren que el manejo silvícola puede afectar el reciclaje de nutrientes por la alteración en la composición de especies y estructura del bosque, aun cuando en el bosque secundario deciduo una extracción selectiva de madera en tiempo reciente (cinco años), no afecta la descomposición de la hojarasca o los montos de mineralización del nitrógeno.

Palabras clave: Andisol, bosque templado lluvioso, Chile, ciclo del nitrógeno, dinámica de nutrientes.

INTRODUCTION

Old-growth Andean forest ecosystems of southern Chile, including *Nothofagus* species, represent an important reserve of temperate forests in the world (Armesto et al. 1998). The combination of low atmospheric nutrient inputs, reduced temperatures, and a high degree of soil organic matter stabilization limits nutrient availability in these mountainous volcanic ecosystems (Matus et al. 2008), so that the input of fresh soil organic matter provides an important nutrient source (Pérez 1996). Litterfall represents the main nutrient transfer process from aboveground plant parts to the soil (Vitousek et al. 1994), and a large amount of dead organic material is produced belowground as well by fine root turnover. Coarse woody debris is another important structural component in temperate forests (Schlegel & Donoso 2008). Ultimately, all this dead plant material can be re-used as an energy source by heterotrophic organisms, and nutrients are recycled into new plant material. The decomposition rate of litter is governed by the interaction between environmental condiditions, substrate quality, and decomposing communities of soil fauna and microorganisms (Santa Regina et al. 1997). Litter decomposition is often negatively related to its initial lignin content (Rutigliano et al. 1995, Vivanco & Austin 2008), and positively related to nitrogen (N) and soil temperature. Initital litter calcium can have a positive effect on the decomposition as well (Hobbie et al. 2006). Besides direct uptake of organic nutrients through mycorrhizal plant associations (Jones et al. 2005), nutrients stored in organic compounds are mainly used by forest vegetation after mineralization. As such, mineralization is a principal process in the production of plant-available nutrients. In pristine south Chilean volcanic rainforest soils, previous studies have indicated optimized N bioavailability by means of N retention mechanisms such as heterotrophic nitrification, dissimilatory nitrate reduction to ammonium, and nitrate turnover into the soil organic matter (Huygens et al. 2008).

One of the major threats for southern temperate forests involves conversion to grassland or monospecific *Pinus* or *Eucalyptus* plantations. This progressive fragmentation also affects the structure and composition of the remaining forest ecosystems (Echeverría et al. 2007). Therefore the management of native temperate forest ecosystems should be oriented towards forest use through the provision of ecosystem services without biological diversity loss (Nahuelhual et al. 2007). Understanding the biogeochemistry of the ecosystem is a prerequisite for such sustainable forest management. To date, only little information is available on the internal nutrient cycle of pristine forests and native secondary forests in south-central Chile. Previous studies in temperate forests in this region have reported a wide range of litterfall and litter decomposition rates (e.g., Veblen et al. 1996, Pérez et al. 1998, Lusk et al. 2001, Leiva & Godoy 2002). Moreover, less is known on the potential nutrient return by litterfall and nutrient dynamics in decomposing litter (Lusk et al. 2003, Decker & Boerner 2006), particularly for nutrients other than N. Discrepancies in microbial N and phosphorus (P) cycling have been found among evergreen and deciduous forests in south Chile (Pérez et al. 1998, Redel et al. 2008). Likewise, forest disturbance can potentially affect nutrient availability and cycling in these forest soils (Pérez et al. 2004, Redel et al. 2008) due to differences in nutrient inputs or turnover. Therefore, the present study aimed to estimate nutrient cycling by litterfall, litter decomposition, and N mineralization in evergreen and deciduous temperate Valdivian rainforests in the lower Andes subject to different degrees of human intervention. The specific objectives were to quantify and compare (i) annual and seasonal litterfall mass and major nutrient fluxes, (ii) decomposition rates and nutrient dynamics of mixed leaf litter and bark litter, and (iii) in situ net N mineralization rates of the mineral topsoil among four Valdivian *Nothofagus* forest stands. As no replicated stands per forest type or management regime were examined, the study should be considered as a descriptive work.

METHODS

Study site

The study was carried out in San Pablo de Tregua (39°35' S, 72°07' W, 600-925 masl), which is located in the lower Andean mountain range of south central Chile. The climate is temperate and rainy with short and dry summers. Mean annual precipitation is 4000-5000 mm while mean annual air temperature equals 9 °C. The maximum mean monthly air temperature is 20 °C in February and the minimum mean air temperature is 5 °C in August, with possibility of snow at higher altitudes. The topography is mountainous. The soil is classified as Andisol, originating from volcanic ashes with an older stratum of pumicitic material with larger diameter sizes, sedimented on steep to moderately sloping andesitic-basaltic rocks with a good infiltration capacity and a high water retention capacity (Tosso 1985). The prevailing vegetation consists of old-growth evergreen and secondary deciduous forests dominated by *Nothofagus* species.

In this forest complex two evergreen and two deciduous stands were selected (Table 1) and in all stands one representative 1000 m^2 plot was established. The evergreen forest includes a pristine stand (EP) and an altered stand (EA) that has undergone anthropogenic disturbance in 1950. As a result, tree species composition and tree number clearly differ between the evergreen stands (Table 1). The dominant tree species are broadleaved evergreen *Nothofagus dombeyi* (Mirb) Oerst., *Laureliopsis philippiana* Looser, and the conifer *Saxegothaea conspicua* Lindl. The secondary deciduous forest includes an unmanaged (DU) and managed (DM) stand, both dominated by *Nothofagus alpina* (Poepp. et Endl) Oerst and *Nothofagus obliqua* (Mirb) Oerst with an age of 55 yr. At the end of the 1940s these deciduous stands were destroyed and burned, followed by a secondary deciduous regeneration of *N. alpina*, representing more than 90 % of the tree number. The density of the DM stand is lower than in the DU stand because of selective cutting in 2002, which removed 35 % of tree basal area and reduced canopy cover by 40 % (Table 1). A dense understory of the bamboo species *Chusquea quila* Kunth is present in DU. The DU stand has a small admixture of evergreen trees (*L. philippiana*), which is not the case in the DM stand (Table 1). Studies on soil P fractions (Redel et al. 2008) and on natural abundance of C and N isotopes (Etcheverría et al. 2009) have been performed in the same four forest stands. Physico-chemical soil characteristics are described by Redel et al. (2008).

Data collection

Litterfall

Litterfall was collected monthly from October 2002 to September 2006. In each of the four plots, twelve 1-m high square collectors of 0.25 m^2 area were set up in a systematic rectangular design. After collection, litterfall was taken to the laboratory, oven-dried (60 °C for 48 h), and weighed. During the first measuring year, litterfall was sorted into six fractions (leaves,

TABLE 1

Characteristics of four forest stands, Andean mountain range, Chile (mean of 3-10 plots of 1000 m^2 per stand): pristine (EP) and altered (EA) evergreen stands, and unmanaged (DU) and managed (DM) deciduous secondary stands. MQD: mean quadratic diameter, i.e. diameter of the tree with mean basal area.

Características de los bosques estudiados, Cordillera de los Andes, Chile (media de 3-10 parcelas de 1000 m^2 por rodal): rodales siempreverdes prístino (EP) y alterado (EA) y bosques deciduos secundarios sin manejo (DU) y con manejo (DM). MQD: diámetro cuadrático promedio, tal como diámetro del árbol con el área basal promedio.

Characteristic	EP	EA	DU	DM
Forest type	Evergreen	Evergreen	Deciduous	Deciduous
Management	Pristine	Altered (1950)	Unmanaged	Managed (2002)
Plot altitude (masl)	805	734	630	637
Slope (%)	12	26	13	27
Composition†	Sc/Lp	Lp/Sc/Mp	Na/Lp	Na/No
Density (trees ha^{-1})	501	873	2300	1030
Basal area (m^2 ha^{-1})	126.9	95.7	50.0	30.1
MQD (cm)	56.8	37.4	22.1	19.3

†Sc: *Saxegothaea conspicua,* Lp: *Laureliopsis philippiana,* Mp: *Myrceugenia planipes,* Na: *Nothofagus alpina*, No: *Nothofagus obliqua*.

bark, reproductive organs, branches, mosses, and remaining material), weighed, and grinded by a Culatti mill to be analyzed chemically. Litterfall of the three other years was not separated.

Litter decomposition

In situ decomposition rates of four leaf litter mixtures and one type of bark litter were determined by a litterbag decomposition experiment during one year (October 2006 - September 2007). In autumn 2006, freshly fallen leaf litter was collected in the four stands, thoroughly hand-mixed and dried (45 °C for 24 h). Per 1000-m^2 study plot in each stand, 20 litterbags were installed on the forest floor within a subplot of 2 x 2 m^2 on 29 September 2006. The nylon litterbags (20 x 20 cm^2 surface area, 2 mm mesh size) were filled with 20 g leaf litter originating from the stand in which they were installed. Additionally, 20 litterbags (6 mm mesh size) containing *Saxegothaea conspicua* bark were installed in a second subplot in the EP stand, as this species periodically releases bark fragments. Per litter type, four litterbags were collected at five time intervals over a one-year period (31, 62, 124, 243, and 363 days after installation). Afterwards, litterbags were dried (45 °C for 48 h) in paper envelopes. Litter was sieved (1 mm) and hand-sorted to remove earth and roots, weighed and finally grinded (Retsch ZM200) for subsequent nutrient analysis. Four subsamples of the five initial litter types were grinded as well.

Nitrogen mineralization

Monthly net N mineralization (N_{min}) of the mineral topsoil was determined in situ in each stand by an incubation experiment during one year (August 2005 - July 2006). At the beginning of each month, six PVC cylinders (7 cm diameter, 10 cm height) were inserted in the soil matrix and sealed at the bottom in order to avoid leaching (Raison et al. 1987). Three PVC tubes were extracted from the field immediately after soil ingression, while the remaining three tubes were extracted at the end of the month (Raison et al. 1987). In the laboratory, the three field replicates were merged into one composite sample, sieved (2 mm), and extracted (1 M KCl, soil to solution ratio 1:3, 1 h).

Chemical analysis

The six different litterfall fractions separated in the first measuring year were analyzed for total N using a modified Kjeldahl method. Litterfall samples were digested by nitric acid (HNO_3; 65 %) and perchloric acid (HClO4; 70 %) in a 1:5 ratio and analysed for K^+, Ca^{2+}, and Mg^{2+} by flame atomic absorption spectrophotometry (Varian SpectrAA-220, USA), while P was determined colorimetrically (Varian Cary 50, USA) in the same digestion by the molybdate method. The nutrient content in leaf litterfall was determined in four composite three-monthly samples per stand, while the other fractions were analyzed after pooling monthly samples into one annual sample. For the litter decomposition experiment, 20 initial samples and 100 individual litterbag samples were analyzed in duplicate for total C and N with an elemental analyzer (ANCA-SL, SerCon, UK) coupled to an isotope ratio mass spectrometer (20-20, SerCon, UK), while K^+, Ca^{2+}, Mg^{2+}, and P were measured as described above. Lignin, hemicellulose, and cellulose contents of composite (four repetitions per type) initial and one-year decomposed litter samples were determined according to Van Soest et al. (1991). Dissolved inorganic N concentrations in soil KCl extracts were measured in triplicate using the steam distillation method (Bremner & Keeny 1965).

Data analysis

Nutrient amounts in litterfall and decomposing litter were calculated by multiplying the nutrient content by the litterfall and remaining litter mass, respectively. Cumulative net N mineralization over one year was calculated as the sum of the differences in dissolved inorganic N (DIN; NH_4-N + NO_3-N) between the end and the beginning of each month (n = 12). Litterfall mass was compared between the stands and between the study years by a non-parametric Friedman test, as normality was not met according to Shapiro-Wilk tests. If the Friedman test indicated at least one significant difference between groups, Wilcoxon signed rank tests were used, which is a non-parametric alternative to paired t-tests. The same approach was used to compare the mass of litterfall fractions between the four stands in the first study year.

Remaining litter mass during decomposition was compared between stands and between decomposition periods with a Kruskal-Wallis test, which is a non-parametric alternative to a one-way ANOVA. If this indicated at least one significant difference between groups, post-hoc tests were performed by Wilcoxon rank sum tests, a non-parametric alternative to two-sample t-tests. As each decomposition data group consisted of four repetitions, the assumption of normality could not be tested and therefore non-parametric tests were used. Litter decomposition rates were determined using single-pool and double-pool exponential decay models (Wieder & Lang 1982):

$$X = A \cdot \exp(-k_1 \cdot t) + (1-A) \cdot \exp(-k_2 \cdot t) \quad (1)$$

where X is the proportion (%) of initial mass at time t (day), A is a constant, and k_1 and k_2 are decay constants. The double-pool exponential model assumes that litter can be partitioned into two components, a relative easily decomposed fraction (A) and a more recalcitrant fraction (1-A) (Wieder & Lang 1982). In the single-pool exponential model A equals 1 and only one decay constant is used. As recommended by Adair et al. (2010), initial litter mass was fixed at the measured value and model parameters were estimated with nonlinear regression. The standard error of the model parameters allowed a statistical comparison of the five litter types. Differences in nutrient amount in the decomposing litter were analyzed using Kruskal-Wallis and Wilcoxon rank sum tests. The N and P concentrations (%) were related to the relative mass loss (%) by single linear regression models. As an indicator of internal K, Ca, and Mg recycling, the element amount released after one year of leaf litter decomposition was calculated from the measurements by multiplying the nutrient input by leaf litterfall with the net nutrient release (% of initial) from leaf litter after one year.

For the N mineralization experiment, Pearson correlation coefficients were calculated to evaluate relationships between dependent variables (NH_4-N, NO_3-N and N_{min}) and microclimatic variables (soil water content and soil temperature) for each stand. A level of $P < 0.05$ was chosen as the minimum for significance. All statistical analyses were done using SPSS 15.0.

RESULTS

Litterfall

Annual litterfall in the four stands ranged from 3487 to 5811 kg ha^{-1} yr^{-1} over the study period (Table 2). No significant difference in mean annual litterfall mass was observed between the two evergreen stands (EP and EA). In the deciduous stands, litterfall was lower in the managed (DM) stand than in the unmanaged (DU) stand (P = 0.002) and lower in DM than in EA (P = 0.034) during the first study year. Over the four years, litterfall differed significantly between DM and the other stands (P < 0.030) and between DM and DU (P < 0.0001). The seasonal evolution of litterfall depended on the forest type (Fig. 1) with the main evergreen litterfall flux (56 %) in January-March and the main deciduous litterfall flux in March and April (63 % in DM and 76 % in DU). Leaves contributed 73 % of total litterfall (Table 3), averaged over the four stands in 2002-2003. The contribution to litterfall was much lower for branches and reproductive organs, and negligible for bark, moss, and miscellaneous material, except for bark litterfall in EP (4 %).

Mass-weighted nutrient content in annual leaf litterfall of 2002-2003 was higher for N (0.9-1.4 %) and Ca (0.8-1.5 %) than for K (0.1-0.5 %), Mg (0.1-0.3 %), and P (0.05-0.08 %). Leaf litterfall content varied more among the evergreen stands than among the deciduous stands, with 2-3 times more K, Ca, and Mg in EA than EP. Branch litterfall contained less N (0.7-0.8 %) and Mg (0.1-0.15 %) than leaf litterfall. The N (1.3-1.6 %) and K (0.2-0.3 %) content in reproductive structures was higher than in leaves. Total nutrient flux in litterfall during 2002-2003 was highest for N (44-69 kg ha^{-1} yr^{-1}) and Ca (39-73 kg ha^{-1} yr^{-1}) (Fig. 2). The litterfall flux of K and Mg was higher in EA than in the other stands because of the higher content in EA leaf litterfall. Litterfall fluxes of P varied little (2.6-3.6 kg ha^{-1} yr^{-1}). As for the litterfall mass, foliage contributed most to litterfall nutrient fluxes (60-92 % for all stands and nutrients; Fig. 2), with an average of 77 %.

Litter decomposition

The initial C content differed significantly between the five litter types (Table 4) and was highest in EP leaf and bark litter and lowest in EA. The N content was similar in all leaf litter types but four times lower in bark, which consequently had a significantly higher C:N ratio than leaf litter. The initial content of P, K, Ca and Mg differed significantly between litter types, with higher K, Ca, and Mg contents in DU than in DM and in EA than in EP. The chemical composition of the initial litter was consistent with the litterfall data.

After one year of decomposition, mean mass loss was 32 % for the four leaf litter types (27-37 %) and only 8 % for bark. Decomposing litter mass was better described by double exponential models (Fig. 3, Table 5) than by single models because of the faster decay

TABLE 2

Litterfall (kg ha^{-1} yr^{-1}) for four forest stands, Andean mountain range, Chile (see Table 1) from October 2002 to September 2006 (CV: coefficient of variation over the four years, in %). Different letters within a column indicate significantly (P < 0.05) different means between stands according to two-tailed Wilcoxon signed rank tests.

Aporte de hojarasca (kg ha^{-1} año^{-1}) para los cuatro rodales estudiados, Cordillera de los Andes, Chile (ver Tabla 1), desde octubre 2002 hasta septiembre 2006 (CV: coeficiente de variación de los cuatro años, en %). Letras diferentes dentro una columna indican diferencias significativas (P < 0.05) entre los promedios de los sitios de acuerdo a la prueba de Wilcoxon de dos colas.

Stand	2002-2003	2003-2004	2004-2005	2005-2006	Mean 2002-2006 (CV)
EP	4895^{ab}	5811	4805	3788	4758^{a} (17)
EA	5139^{a}	4233	4428	4421	4573^{ab} (10)
DU	5777^{a}	5302	4460	4770	5058^{ac} (11)
DM	3556^{b}	5076	4068	4459	4273^{d} (16)

during the first month. Almost no significant differences in decomposing leaf litter mass were found between the stands, except during the first two months. The labile fraction of litter (A) tended to be smaller for DM and bark litter (4-7 %) compared to the other litter types (11-17 %) (Table 5). Estimated decay of this labile pool (k_1) was significantly slower for leaf litter of EP and DU than for DM and bark litter. The more recalcitrant pool (k_2) decomposed significantly slower for bark litter than for EA and DM leaf litter. Carbon dynamics of the litter (Appendix) were similar to mass loss dynamics.

Nutrient dynamics in decomposing litter depended on the nutrient and litter type (Fig. 4, Appendix). During the first months of decomposition the remaining N amount tended to decline in evergreen litter, in contrast to a net N increase in deciduous litter and bark litter (Fig. 4A). Net N amounts in deciduous litter after 8-12 months equalled the initial values (Appendix). The N content (%) in decomposing leaf litter increased significantly with mass loss (Fig. 5A, $P < 0.001$, $R^2 = 0.47$-0.82). As a result of the relatively restricted N dynamics and decreasing C amounts, the C:N

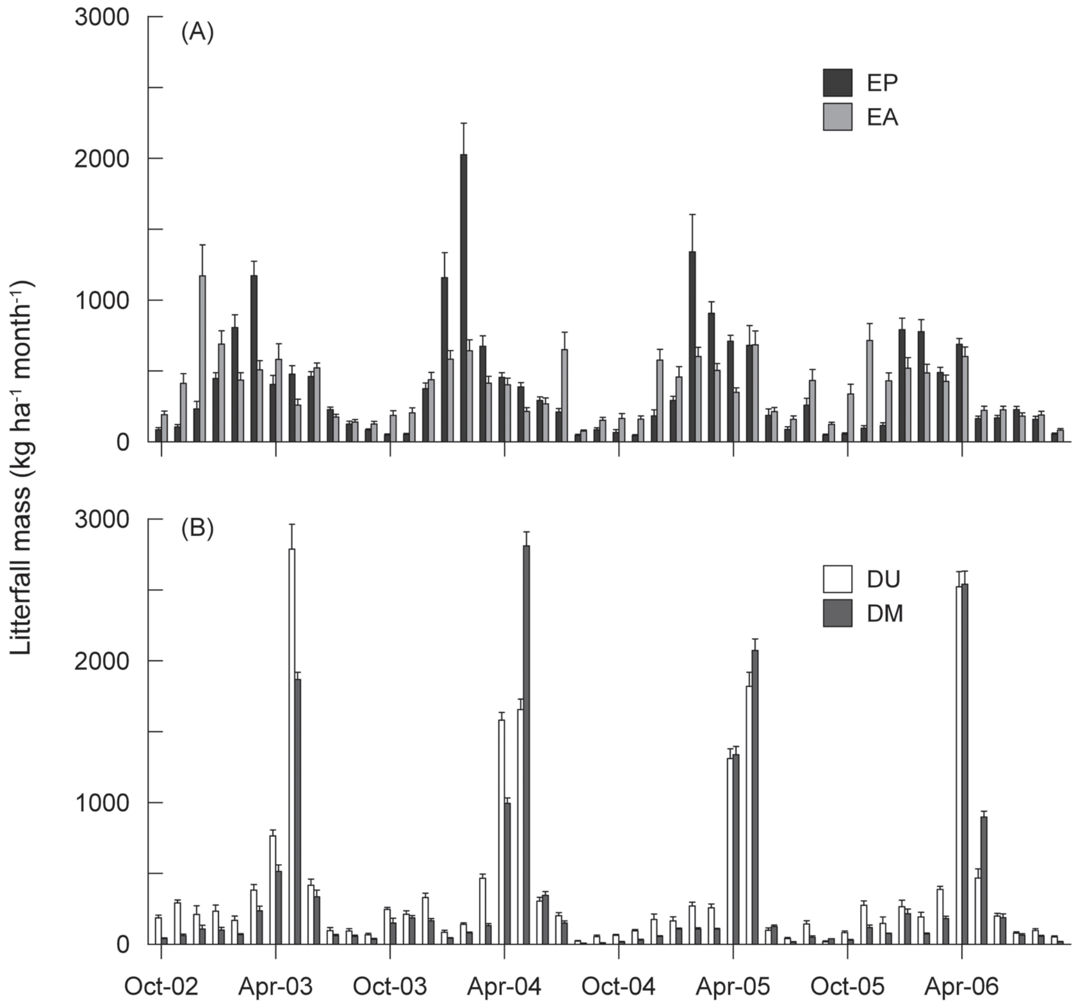

Fig. 1: Litterfall mass (kg ha^{-1} month^{-1}) from October 2002 to September 2006 in (A) two evergreen forests stands and (B) two secondary deciduous forest stands, Andean mountain range, Chile (see Table 1 for abbreviations). Bars show means ± SE (n = 12).

Masa de hojarasca (kg ha^{-1} mes^{-1}) desde octubre 2002 hasta septiembre 2006 en (A) dos bosques siempreverdes y (B) dos bosques secundarios deciduos, Cordillera de los Andes, Chile (ver Tabla 1 para abreviaciones). Columnas muestran mediciones de media ± EE (n = 12).

ratio decreased significantly over time in all leaf litter (Fig. 4B, Appendix), in contrast to the bark litter. After 8-12 months the C:N ratios were significantly higher in evergreen litter than in deciduous litter. As for N, the remaining amount of P initially decreased in the evergreen stands and increased in the deciduous stands (Fig. 4C, Appendix). With increasing mass loss the P content in leaf litter increased (Fig. 5B, $P < 0.05$, $R^2 = 0.19$-0.44), while in bark litter it decreased (Fig. 5B, $P < 0.001$, $R^2 = 0.48$). The amount of lignin after one year was similar as initially for all the litter types, while hemicellulose and cellulose decreased by 36-44 % compared to the initial amount, except for EP leaf litter (Table 4).

TABLE 3

Flux (kg ha^{-1} yr^{-1}) and contribution (%, in brackets) of six litterfall fractions from October 2002 to September 2003 for four forest stands, Andean mountain range, Chile (see Table 1). Different letters within a row indicate significantly ($P < 0.05$) different means between stands according to two-tailed Wilcoxon signed rank tests.

Flujo (kg ha^{-1} $año^{-1}$) y contribución (%, en paréntesis) de seis fracciones de hojarasca desde octubre 2002 hasta septiembre 2003, para los cuatro rodales estudiados, Cordillera de los Andes, Chile (ver Tabla 1). Letras diferentes dentro de una fila indican diferencias significativas ($P < 0.05$) entre los promedios de los sitios de acuerdo al tests de Wilcoxon de dos colas.

Fraction	EP	EA	DU	DM
Leaves	3252[a] (66)	4168[a] (81)	4419[ab] (77)	2482[ac] (70)
Branches	856 (18)	530 (10)	931 (16)	833 (23)
Reproductive organs	544[a] (11)	290[bc] (5.6)	383[ac] (6.6)	199[a] (5.6)
Bark	197[a] (4.0)	70[b] (1.4)	24[c] (0.4)	25[c] (0.7)
Moss	32[a] (0.7)	63[b] (1.2)	9[c] (0.2)	14[c] (0.4)
Miscellaneous	15 (0.3)	18 (0.4)	11 (0.2)	5 (0.1)
Total	4895[a] (100)	5139[ab] (100)	5777[ab] (100)	3556[ac] (100)

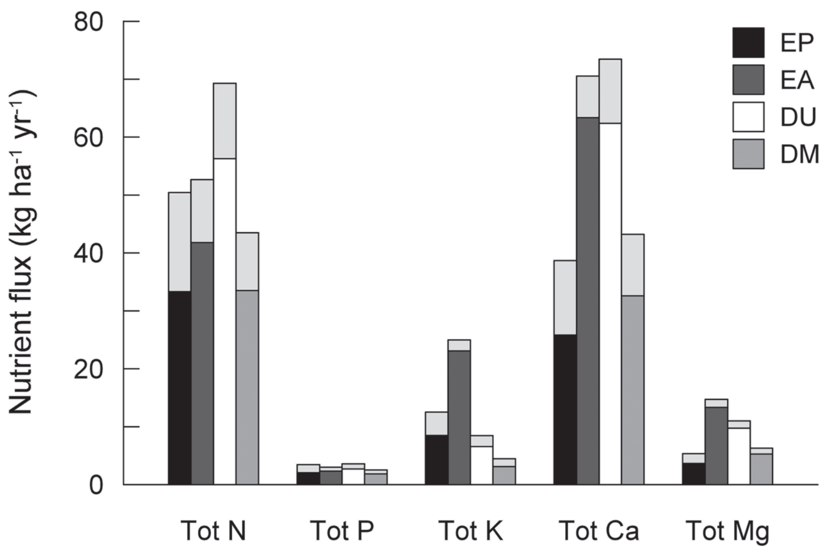

Fig. 2: Nutrient fluxes (kg ha^{-1} yr^{-1}) in litterfall from October 2002 to September 2003 in four forest stands, Andean mountain range, Chile (see Table 1). Bottom bars show leaf litterfall, top bars represent the sum of the other litterfall fractions (see Table 3).

Flujos de nutrientes (kg ha^{-1} $año^{-1}$) en hojarasca desde octubre 2002 hasta septiembre 2003 en cuatro bosques, Cordillera de los Andes, Chile (ver Tabla 1). Columnas inferiores indican el aporte de hojas en la hojarasca, columnas superiores representan la suma de las otras fracciones de la hojarasca (ver Tabla 3).

The amount of K, Ca, and Mg in decomposing litter generally decreased during the decay, remaining relatively higher in deciduous litter than in evergreen litter (Fig. 4D, 4E, and 4F). After eight months of decomposition, the K amount was similar (P > 0.05) in all leaf litter types (Appendix). The Ca amount decreased gradually after a marked initial loss (Fig. 4E). Despite twofold initial Ca contents in EA compared to EP litter, a similar relative decrease in Ca (to 29-37 %) was found, in contrast to the deciduous litter. The amount of Mg (Fig. 4F) decreased to 26-46 % in evergreen leaf litter after one year, while the decline was lower in deciduous litter (63-64 %). The sum of the calculated K, Ca, and Mg release by leaf litterfall after one year of decomposition was four times higher in EA (4.1 $kmol_c$ ha^{-1} yr^{-1}) than in the other three stands (0.5-0.7 $kmol_c$ ha^{-1} yr^{-1}).

Nitrogen mineralization

The highest cumulative net N mineralization (11.3 kg N ha^{-1} yr^{-1}) was found in EP, while EA had the lowest cumulative mineralization (1.7 kg N ha^{-1} yr^{-1}) and the deciduous forest soils were intermediate (10.5 (DM) and 7.1 (DU) kg N ha^{-1} yr^{-1}; Fig. 6). A seasonal trend in cumulative N mineralization was observed with increased rates in EP, DU, and DM at the beginning of spring (September-October), and net N immobilization during the austral summer (December-January). The monthly values of NH_4-N, NO_3-N and N_{min} for evergreen and deciduous forest soils were not significantly related to soil temperature (r < 0.31; P > 0.15) and soil moisture (r < 0.35; P > 0.10).

DISCUSSION

Observed annual litterfall (Table 1) in four forest stands in San Pablo de Tregua was within the range (1.7 to 7.4 ton ha^{-1} yr^{-1}) reported for temperate forests in south-central Chile (Veblen et al. 1996, Pérez et al. 1998, Leiva & Godoy 2002). Mean litterfall in the evergreen stands was lower than in a *Nothofagus dombeyi - N. alpina* forest in the Andean range (5.4 ton ha^{-1} yr^{-1}; Burschel et al. 1976) and a *N. dombeyi - N. alpina - L. philippiana - S. conspicua* forest (Veblen et al. 1996). Litterfall in the deciduous unmanaged stand was lower than in other *N. alpina* stands (5.4-5.9 ton ha^{-1} yr^{-1}; González & Donoso 1999). The significantly lower litterfall in the managed deciduous stand compared to the unmanaged deciduous stand was mainly caused by lower leaf litterfall, which was

TABLE 4

Initial composition (mean ± SD, n = 4; except for lignin, hemicellulose, and cellulose, n = 1) of leaf litter in four forest stands (see Table 1) and of *Saxegothaea conspicua* bark litter in EP, Andean mountain range, Chile (see Table 1). Values in brackets give the remaining fraction (% of initial content) of lignin, hemicellulose and cellulose after one year of decomposition. Different letters within a column indicate significantly (P < 0.05) different means between stands according to Wilcoxon signed rank tests.

Composición inicial (media ± DE, n = 4, excepto para lignina, hemicelulosa y celulosa, n = 1) de la hojarasca en cuatro rodales (ver Tabla 1) y corteza de *Saxegothaea conspicua* en EP, Cordillera de los Andes, Chile (ver Tabla 1). Valores en paréntesis corresponden a la fracción remanente (% del contenido inicial) de lignina, hemicelulosa y celulosa después de un año de descomposición. Letras diferentes dentro una columna indican diferencias significativas (P < 0.05) entre los promedios de los sitios de acuerdo a la prueba de Wilcoxon.

Litter	C (%)	N (%)	C:N (-)	P (mg g^{-1})	K (mg g^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})	Lignin (%, % of initial)	Hemicellulose (%, % of initial)	Cellulose (%, % of initial)
EP	47.3^a ± 0.3	1.23^a ± 0.07	39^a ± 2	0.72^a ± 0.02	2.48^a ± 0.22	7.04^a ± 0.13	1.13^a ± 0.05	27.7 (102)	13.1 (100)	19.7 (92)
EA	42.1^b ± 0.4	1.22^a ± 0.04	35^b ± 1	0.60^b ± 0.01	6.75^b ± 0.27	14.5^b ± 0.43	4.15^b ± 0.19	11.5 (90)	18.4 (64)	20.0 (66)
DU	44.7^c ± 0.5	1.23^a ± 0.02	36^b ± 1	0.54^c ± 0.01	1.51^c ± 0.17	12.4^c ± 0.24	1.86^c ± 0.05	26.9 (114)	17.3 (64)	22.6 (60)
DM	44.9^c ± 1.8	1.21^a ± 0.10	37^{ab} ± 2	0.57^d ± 0.01	0.63^d ± 0.10	10.7^d ± 0.34	1.40^d ± 0.03	22.3 (83)	16.8 (60)	19.3 (62)
Bark	47.5^a ± 0.5	0.34^b ± 0.01	141^c ± 5	0.17^e ± 0.01	0.33^e ± 0.03	6.37^e ± 0.33	0.49^e ± 0.03	32.3 (93)	10.2 (56)	36.6 (62)

almost halved in the first year after tree harvesting due to the lower basal area in the managed stand and the absence of litterfall of *Chusquea*, an understorey species that was removed before selective cutting. The contribution of leaves to total litterfall in the present study agreed well with values of 60-76 % in forests worldwide (Bray & Gorham 1964). Our study does not confirm a higher share of the leaf fraction in secondary forest than in pristine forest (Rodríguez et al. 2001). The high contribution of leaves in the altered evergreen stand may be due to the dense understorey of bamboo with a relatively higher leaf share compared to trees. Bark contributed most to litterfall in the evergreen pristine stand because of the presence of *S. conspicua*, which periodically releases bark fragments (up to 130 kg^{-1} ha^{-1} yr^{-1}; R. Godoy, unpublished data), and for this reason was used in the litter decomposition experiment.

By human intervention the tree species composition and thus litter nutrient content differed among the two evergreen stands and among the two deciduous stands. In leaf litterfall, nutrient contents varied more among the evergreen stands because of their more different tree species composition than the deciduous stands. Leaves and branches had higher N and Ca contents than other fractions, in line with Zimmermann et al. (2002). The lower P content in deciduous than evergreen foliage litter can reflect the lower total and available P content in the deciduous forest soils, as reported by Redel et al. (2008). The higher content of K, Ca and Mg in the leaf litter of the altered evergreen stand may result from the presence of the understorey species *Myrceugenia planipes* (Hooker et Arnott) and *Amomyrtus luma* (Mol.) Legr. et. Kraus, which were absent in the other stands. The mean decomposition rate of leaf litter after one year (32 %) was similar in the four stands, and was consistent with the range reported for other temperate forests (Pérez et al. 2010). There was no clear effect of human intervention or evergreen versus deciduous forest type, except for the faster initial leaf litter decomposition in the deciduous stand with previous selective cutting, than in the unmanaged stand. This contrasts to Caldentey et al. (2001), who found a higher decomposition rate in a *N. pumilio* shelterwood system than in an unmanaged stand. After the fast initial decomposition of a small labile fraction, *S. conspicua* bark litter decomposed four times slower than leaf litter. The rapid initial mass and C loss in all litter types can be attributed to the decomposition of easily degradable carbohydrates and soluble compounds. The initial C:N ratios were in the same narrow range in all leaf litter mixtures but four times higher in bark, which confirms the impact of substrate quality on the decomposition rate. Other studies have

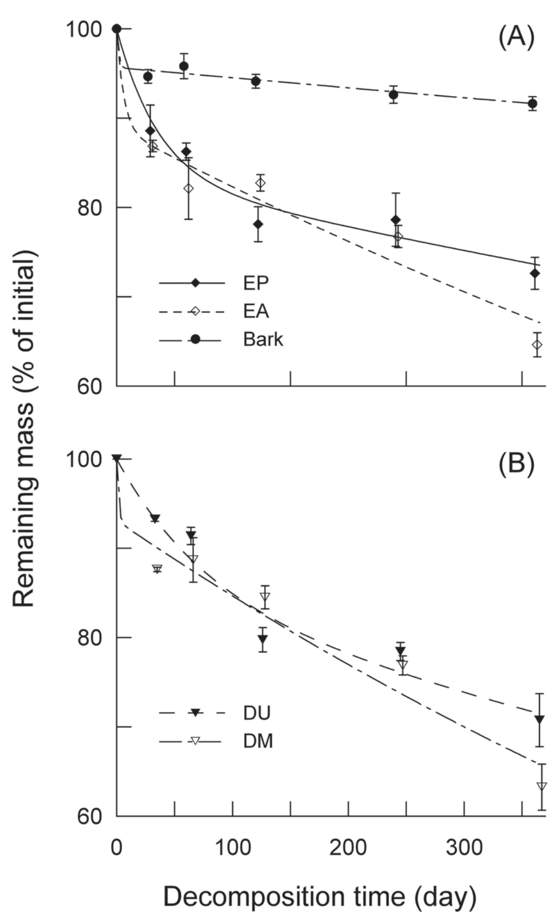

Fig. 3: Percent remaining (A) leaf litter in two evergreen stands and bark litter in EP, and (B) leaf litter in two deciduous stands, Andean mountain range, Chile (see Table 1) during decomposition. Dots are measured means ± SE (n = 4), lines represent modelled double-pool exponential functions (see Table 5).

Porcentaje remanente (A) de hojas en la hojarasca en dos bosques siempreverdes y corteza en EP y (B) de hojas en la hojarasca de bosques secundarios deciduos, Cordillera de los Andes, Chile (ver Tabla 1), durante la descomposición. Los puntos son mediciones de media ± EE (n = 4) y líneas representan la función exponencial modelada (ver Tabla 5).

reported leaf litter decay rates of species included in the present study. Mass loss of *N. obliqua* varied from 6 % after one year (Decker & Boerner 2006) to 40 % after six months (Lusk et al. 2001), suggesting that different environmental conditions and study designs influence decay rates. For *N. dombeyi* a decay of 19 % has been found (Decker & Boerner 2006, Lima et al. 1994) and for *L. philippiana* and *N. nitida* a 13-month mass loss of 60-90 and 40 %, respectively (Pérez 1996). Mass loss often increases if litter of different species is mixed (Gartner & Cardon 2004), but the present comparison does not allow assessing a potential effect on decomposition of mixed vs. single-species litter.

The C amount in decomposing litter decreased at the same rate as the mass loss as C was degraded and incorporated by microorganisms or respired to CO_2. The constant litter C content indicates that C was not limiting decomposition (Domisch et al. 2008). The N and P contents, in contrast, increased linearly with leaf litter loss (cf. McClaugherty & Berg 1987, Coûteaux et al. 1998). Evergreen leaf litter showed initial net N and P mineralization, while in deciduous litter net accumulation was observed first. Net accumulation of N may be due to N_2 fixation by free living diazotrophs, throughfall, insect frass, fungal translocation, and microbial immobilization (Melillo et al. 1982). Given the low throughfall of DIN to the forest floor at the study site (~1.7 kg N ha^{-1} yr^{-1}, Staelens et al. 2005), this input likely contributed little to N accumulation. As bacteria and fungi have a lower C:N ratio compared to litter, litter N is immobilized by these microorganisms during decomposition, thereby increasing the N content (Salamanca et al. 1998). Potassium showed a rapid decrease in the initial stage of decomposition (cf. Gosz et al. 1976, van Wesemael 1993, Santa Regina et al. 1997), because K is not bound as a structural component in plants and is highly water soluble. In contrast, the Ca amount generally decreased slowly over time, mainly in evergreen leaf litter, likely due to the association of Ca with resistant compounds or inclusion within cell walls (Santa Regina et al. 1997). Our results did not confirm that mass loss was significantly related to litter Ca contents, as found by Hobbie et al. (2006).

The obtained net N mineralization rates are similar to reports for mixed *Nothofagus* forests in the Central Valley of Chile (6 kg N ha^{-1} yr^{-1}; Cárcamo et al. 2004) and a *N. obliqua* stand in southern Chile (Rivas et al. 2009). Higher rates (12-37 kg N ha^{-1} yr^{-1}) have been found for old-growth evergreen forest (Pérez et al. 2003) and *Nothofagus* and *Fitzroya* forests on Chiloé Island (Chile) (Pérez et al. 1998). All these rates are considerably lower than for temperate forest soils in the northern hemisphere with reported values of up to 130 kg N ha^{-1} yr^{-1} (Reich et al. 1997). Climate factors typically induce a seasonal trend in net N mineralization (MacDonald et al. 1995). As such, in situ N mineralization rates of *Nothofagus betuloides* (Mirb.) Oerst. soils were

TABLE 5

Parameters (mean ± SE) and determination coefficients of double-pool exponential decomposition models for leaf litter in four forest stands (see Table 1) and *Saxegothaea conspicua* bark litter in EP, Andean mountain range, Chile. Different letters within a column indicate significantly (P < 0.05) different means between litter types according to 95 % confidence intervals.

Parámetros (media ± EE) y coeficiente de determinación de los modelos exponencial pool- doble de descomposición para litera de hojas en cuatro rodales (ver Tabla 1) y corteza de *Saxegothaea conspicua* en EP, Cordillera de los Andes, Chile. Letras diferentes dentro de una columna indican diferencias significativas (P < 0.05) entre los promedios de los tipos de hojarasca de acuerdo a intervalos de confianza de 95 %.

Litter	A	k_1	k_2	R^2
EP	16.7 ± 5.1	0.028^{a} ± 0.016	0.00034^{ab} ± 0.00022	0.635
EA	11.1 ± 2.2	0.167^{ab} ± 0.350	0.00077^{a} ± 0.00014	0.781
DU	15.3 ± 11.9	0.013^{a} ± 0.012	0.00047^{ab} ± 0.00040	0.849
DM	6.9 ± 1.6	0.645^{b} ± 0.001	0.00095^{a} ± 0.00013	0.848
Bark	4.3 ± 0.7	0.610^{b} ± 0.001	0.00012^{b} ± 0.00003	0.390

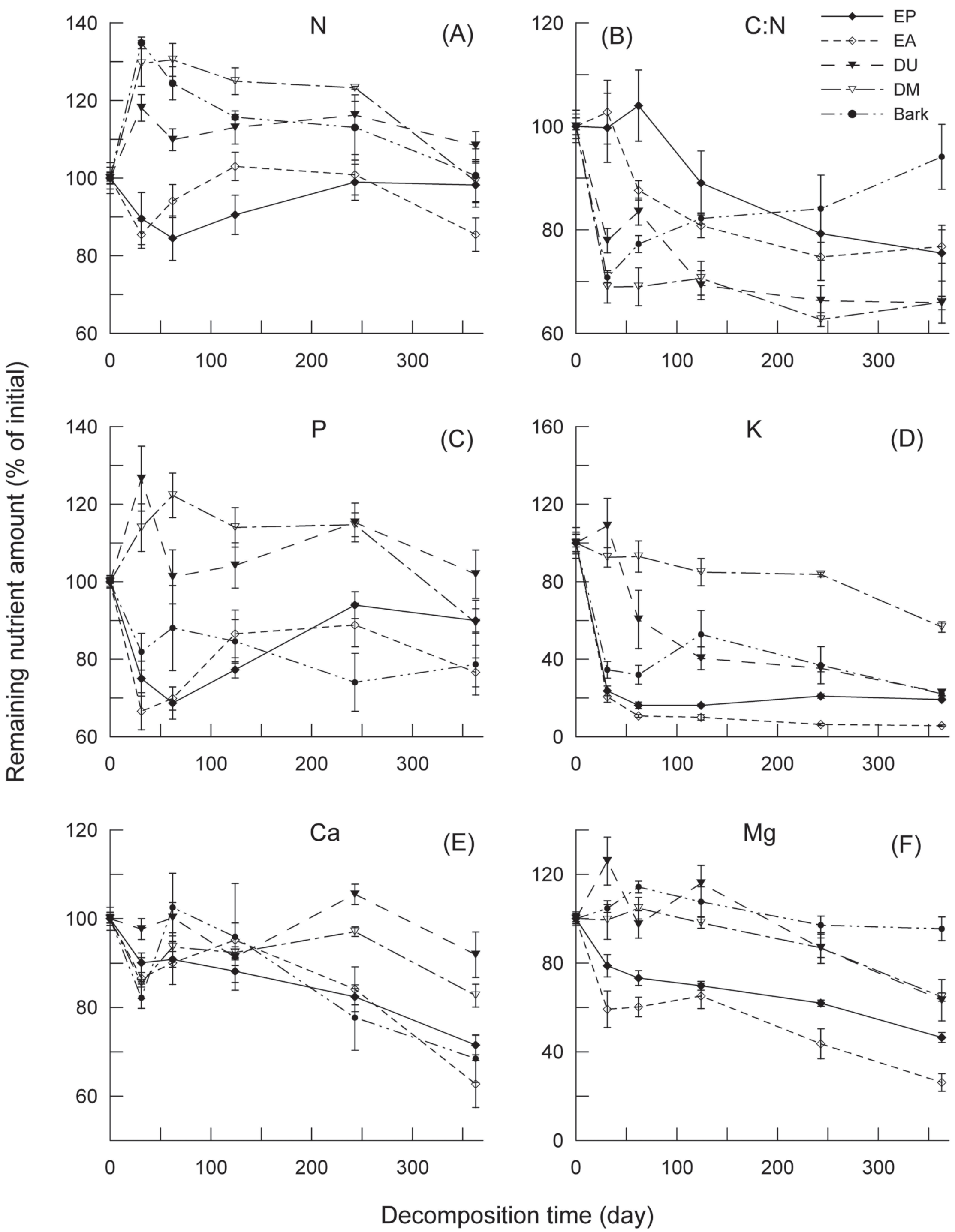

Fig. 4: Remaining nutrient amount (% of initial) and C:N ratio of leaf litter in four forest stands and bark litter in EP, Andean mountain range, Chile (see Table 1) during decomposition. Dots are measured means ± SE (n = 4).

Contenido remanente de nutrientes (% del inicial) y radio C:N de hojas en la hojarasca en cuatro tipos de bosques y corteza en EP, Cordillera de los Andes, Chile (ver Tabla 1), durante la descomposición. Los puntos son mediciones de media ± EE (n = 4).

low during the cold humid winter months (Rivas et al. 2007). When temperature rose in spring, net mineralization increased in our study, similarly to N mineralization studies in *Aextoxicon punctatum* Ruiz et Pav. forest soils from north-central and south-central Chile (Pérez 1996). The alleviation of N mineralization during summer can be explained by inorganic N absorption by roots and eventual immobilization in microbial biomass (Nunan et al. 2000).

Primary production in temperate forest ecosystems depends on internal cycling of nutrients by litterfall and consequent decomposition of organic material. The present study quantified that considerable fluxes of organically-bound nutrients occur via litterfall, and mainly through leaves, followed

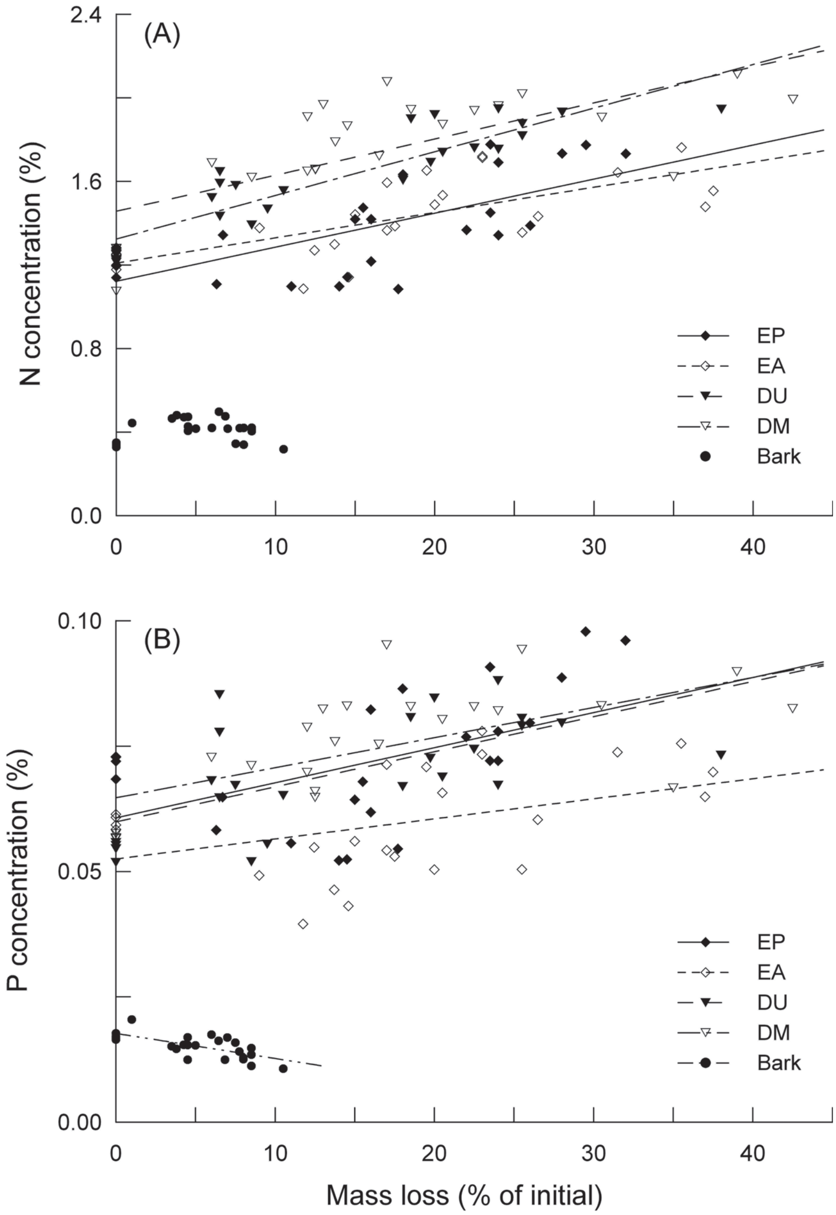

Fig. 5: Concentration (%) of (A) N and (B) P in decomposing leaf litter of four forest stands and bark litter in EP, Andean mountain range, Chile (see Table 1) in relationship to mass loss (% of initial litterbag mass).

Concentración (%) de (A) N y (B) P en hojas de la hojarasca en descomposición de cuatro tipos de bosques y corteza en EP, Cordillera de los Andes, Chile (ver Tabla 1), en relación a la pérdida de masa (% de masa inicial en las litterbags).

by a net K, Ca, and Mg release during litter decomposition. Combining this potential nutrient return by leaf litterfall with the nutrient release after one year of decomposition indicated a faster recycling of K, Ca, and Mg in the evergreen altered stand than in the three other study stands. However, next to litter-derived K, Ca, and Mg, canopy leaching in throughfall contributes to the nutrient cycling of these elements (Staelens et al. 2008). The N flux in evergreen litterfall, which peaked during summer, was higher than in evergreen *Fitzroya* and *Nothofagus* forests in the Chilean Coastal mountain range (11-23 kg N ha^{-1} yr^{-1}; Pérez et al. 1998). Nutrient fluxes in leaf litterfall in the unmanaged deciduous stand were similar as in a *N. obliqua* stand in south-central Chile (Staelens et al. 2003, 2005). The lower litterfall N flux in the evergreen stands than in the deciduous stands could indicate more efficient N cycling in the evergreen stands (Pérez et al. 2003). Mass decomposition after one year was not significantly influenced by leaf litter type, which may be due to the fact that the initial leaf litter C:N ratios were relatively high and in the same range. Net N slightly decreased in decomposing evergreen leaf litter and accumulated in deciduous leaf litter, but meaningful net N and P release is expected over longer time-scales (Likens 2003). The highest net N mineralization rate was measured in the soil of the pristine evergreen stand. This is in line with Yan et al. (2009), who found high net N mineralization rates in climax forests. In contrast, soil net N mineralization was low in the altered evergreen stand. Further research with a larger number of field replicates and measurements of the composition of the soil microbial community would be valuable to study soil N processes into more detail.

This study in Valdivian *Nothofagus* rainforests suggests that nutrient cycling was partly influenced by a historical disturbance in the evergreen forest stand via an altered tree species composition and forest structure. Selective cutting in the secondary deciduous stand temporarily decreased litterfall, but did not affect litter decomposition or soil net N mineralization rates four to six years later. However, only one forest stand per combination of forest type and management regime was studied, so that the results should be interpreted with care. While all stands were located close to each other in the same forest complex, potential differences in nutrient cycling cannot be solely attributed to forest type or management, but could be partly related to local stand conditions.

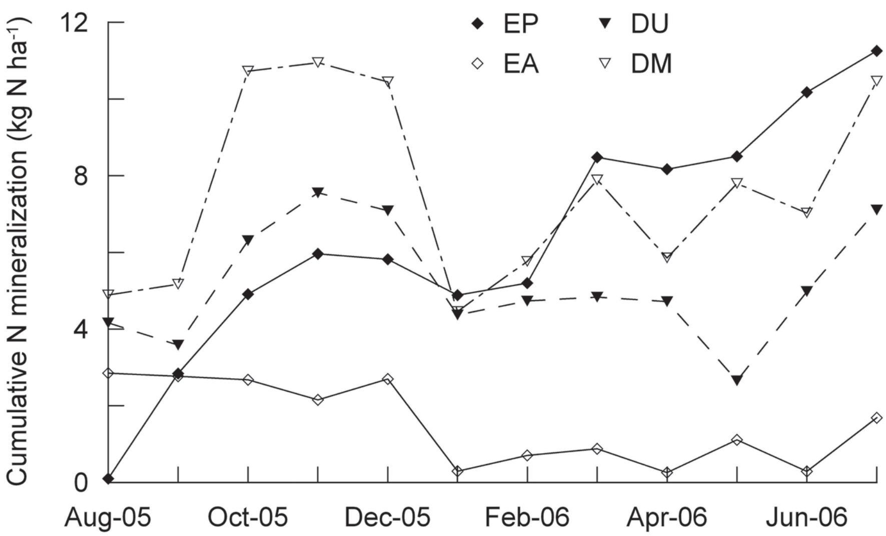

Fig. 6: Cumulative net nitrogen mineralization (kg N ha^{-1} yr^{-1}) from August 2005 to July 2006 in four forest stands, Andean mountain range, Chile (see Table 1).

Mineralización de nitrógeno neta acumulada (kg N ha^{-1} $año^{-1}$) desde agosto 2005 hasta julio 2006 de cuatro tipos de bosques, Cordillera de los Andes, Chile (ver Tabla 1).

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APPENDIX

Remaining nutrient amount and C:N ratio (mean ± SD, n = 4) in litterbags with leaf litter in four forest stands (see Table 1) and *Saxegothaea conspicua* bark litter in EP , after 0 to 12 months of decomposition, Andean mountain range, Chile. Per nutrient, different small letters within a row indicate significant (P < 0.05) differences in nutrient amount between litter types, different capital letters within a column indicate significant differences between decomposition periods.

Contenido de nutrientes remanentes y razón C:N (media ± DE, n = 4) en "litterbags" con hojarasca en los cuatro bosques y corteza de *Saxegothaea conspicua* en EP después de 0 hasta 12 meses de descomposición, Cordillera de los Andes, Chile. Para los nutrientes, letras minúsculas diferentes dentro de una columna indican diferencias significativas (P < 0.05) en el monto de nutrientes entre los tipos de hojarasca, letras mayúsculas diferentes en una misma columna, indican diferencias significativas entre períodos de descomposición.

Element	Month	EP	EA	DU	DM	Bark
C	0	$9.5^{aA} \pm 0.1$	$8.4^{bA} \pm 0.1$	$8.9^{cA} \pm 0.1$	$9.0^{cA} \pm 0.4$	$9.5^{aA} \pm 0.1$
(g bag^{-1})	1	$8.4^{aB} \pm 0.5$	$7.3^{bB} \pm 0.3$	$8.2^{aB} \pm 0.1$	$8.0^{aB} \pm 0.1$	$9.1^{cB} \pm 0.2$
	2	$8.2^{aB} \pm 0.1$	$6.9^{bBC} \pm 0.6$	$8.2^{aB} \pm 0.2$	$8.1^{abB} \pm 0.5$	$9.1^{cB} \pm 0.2$
	4	$7.6^{aBC} \pm 0.4$	$7.0^{bB} \pm 0.3$	$7.0^{bC} \pm 0.3$	$7.9^{aB} \pm 0.5$	$9.0^{cB} \pm 0.2$
	8	$7.4^{aCD} \pm 0.4$	$6.3^{bC} \pm 0.2$	$6.9^{abC} \pm 0.3$	$7.0^{aC} \pm 0.3$	$8.9^{cB} \pm 0.1$
	12	$7.0^{aD} \pm 0.3$	$5.5^{bD} \pm 0.2$	$6.4^{acC} \pm 0.5$	$5.9^{bcC} \pm 0.4$	$8.9^{dB} \pm 0.1$
N–	0	$245^{aA} \pm 14$	$244^{aA} \pm 8$	$247^{aA} \pm 4$	$243^{aA} \pm 19$	$68^{bA} \pm 2$
(mg bag^{-1})	1	$220^{aA} \pm 33$	$208^{aB} \pm 17$	$291^{bB} \pm 17$	$314^{bB} \pm 29$	$91^{cB} \pm 2$
	2	$207^{aA} \pm 28$	$229^{aAB} \pm 21$	$271^{cB} \pm 14$	$317^{bB} \pm 21$	$84^{dBC} \pm 6$
	4	$222^{aA} \pm 25$	$251^{acA} \pm 18$	$279^{bcB} \pm 21$	$303^{bB} \pm 17$	$78^{dC} \pm 1$
	8	$242^{aA} \pm 23$	$246^{aAB} \pm 25$	$287^{bB} \pm 18$	$299^{bB} \pm 2$	$76^{cABC} \pm 11$
	12	$241^{abA} \pm 28$	$208^{aB} \pm 21$	$267^{bAB} \pm 18$	$241^{abA} \pm 25$	$68^{cAC} \pm 9$
C:N	0	$39^{aA} \pm 2$	$35^{bA} \pm 1$	$36^{aA} \pm 0$	$37^{aA} \pm 2$	$141^{cA} \pm 5$
(-)	1	$39^{aB} \pm 5$	$36^{aA} \pm 4$	$28^{bBC} \pm 2$	$26^{bB} \pm 2$	$99^{cB} \pm 3$
	2	$40^{aB} \pm 5$	$30^{bB} \pm 1$	$30^{abB} \pm 2$	$26^{cB} \pm 3$	$109^{dC} \pm 5$
	4	$34^{aB} \pm 5$	$28^{bB} \pm 2$	$25^{bCD} \pm 2$	$26^{aB} \pm 2$	$116^{cCD} \pm 3$
	8	$31^{aB} \pm 4$	$26^{abB} \pm 3$	$24^{bCD} \pm 2$	$23^{bB} \pm 1$	$118^{cABC} \pm 18$
	12	$29^{aB} \pm 4$	$27^{abB} \pm 2$	$24^{bD} \pm 1$	$25^{abB} \pm 3$	$132^{cAD} \pm 18$
P	0	$14.3^{aA} \pm 0.4$	$12.0^{bA} \pm 0.3$	$10.9^{dA} \pm 0.3$	$11.4^{cA} \pm 0.1$	$3.4^{eA} \pm 0.1$
(mg bag^{-1})	1	$10.7^{abBC} \pm 1.3$	$8.0^{aB} \pm 1.2$	$13.8^{cB} \pm 1.8$	$12.9^{bcAB} \pm 1.4$	$2.8^{dB} \pm 0.3$
	2	$9.8^{acB} \pm 1.2$	$8.4^{aB} \pm 0.7$	$11.0^{cAB} \pm 1.5$	$13.9^{bB} \pm 1.3$	$3.0^{dAB} \pm 0.7$
	4	$11.1^{aB} \pm 0.6$	$10.4^{aAB} \pm 1.5$	$11.3^{aAB} \pm 1.3$	$13.0^{aB} \pm 1.2$	$2.9^{bB} \pm 0.4$
	8	$13.4^{aAC} \pm 1.0$	$10.7^{bAB} \pm 1.4$	$12.5^{abBC} \pm 1.1$	$13.0^{aB} \pm 0.7$	$2.5^{cB} \pm 0.5$
	12	$12.9^{aAC} \pm 0.9$	$9.2^{bB} \pm 0.9$	$11.1^{abAC} \pm 1.4$	$10.2^{bA} \pm 1.3$	$2.7^{cB} \pm 0.5$
K	0	$49.6^{aA} \pm 4.3$	$135.0^{bA} \pm 5.4$	$30.2^{dA} \pm 3.4$	$12.6^{cA} \pm 2.0$	$6.5^{eA} \pm 0.6$
(mg bag^{-1})	1	$11.7^{aB} \pm 2.5$	$27.9^{bB} \pm 7.7$	$32.8^{bA} \pm 8.5$	$11.6^{aAB} \pm 1.3$	$2.3^{cB} \pm 0.6$
	2	$8.0^{aBC} \pm 1.7$	$14.5^{abC} \pm 1.9$	$18.3^{bAB} \pm 9.1$	$11.7^{abAB} \pm 2.0$	$2.1^{cBC} \pm 0.6$
	4	$8.0^{aC} \pm 0.6$	$13.5^{bCD} \pm 3.8$	$12.2^{abB} \pm 3.5$	$10.7^{bAB} \pm 1.8$	$3.5^{cB} \pm 1.6$
	8	$10.4^{aB} \pm 1.1$	$8.6^{aDE} \pm 1.4$	$10.6^{aB} \pm 1.1$	$10.5^{aB} \pm 0.3$	$2.4^{bBC} \pm 1.3$
	12	$9.5^{aB} \pm 0.5$	$7.7^{abE} \pm 1.1$	$6.9^{bC} \pm 0.9$	$7.1^{bC} \pm 0.7$	$1.4^{cC} \pm 0.2$
Ca	0	$141^{aA} \pm 3$	$291^{bA} \pm 9$	$248^{dA} \pm 5$	$214^{cA} \pm 7$	$127^{eA} \pm 7$
(mg bag^{-1})	1	$127^{aBC} \pm 6$	$252^{bB} \pm 27$	$242^{bAB} \pm 12$	$183^{cA} \pm 27$	$105^{dB} \pm 6$
	2	$128^{aB} \pm 5$	$262^{bcAB} \pm 28$	$249^{cAB} \pm 17$	$200^{bA} \pm 25$	$131^{aAB} \pm 20$
	4	$124^{aBC} \pm 7$	$277^{bAB} \pm 22$	$227^{dB} \pm 9$	$198^{cA} \pm 18$	$122^{aAB} \pm 31$
	8	$116^{aC} \pm 5$	$245^{bcB} \pm 29$	$262^{cA} \pm 11$	$208^{bA} \pm 9$	$99^{bAB} \pm 19$
	12	$101^{aD} \pm 6$	$183^{bC} \pm 31$	$228^{cAB} \pm 25$	$177^{bB} \pm 8$	$87^{bB} \pm 14$
Mg	0	$22.7^{aA} \pm 0.9$	$83.0^{bA} \pm 3.9$	$37.3^{dA} \pm 1.0$	$28.0^{cAB} \pm 0.7.0$	$9.9^{eA} \pm 0.6$
(mg bag^{-1})	1	$17.9^{aBC} \pm 2.3$	$49.2^{bB} \pm 13.6$	$47.0^{bB} \pm 8.1$	$27.9^{cAB} \pm 4.9$	$10.3^{dAB} \pm 0.4$
	2	$16.6^{aB} \pm 1.5$	$50.0^{bB} \pm 7.3$	$36.3^{bcABC} \pm 4.6$	$29.3^{cA} \pm 2.7$	$11.3^{dB} \pm 0.5$
	4	$15.8^{aB} \pm 0.9$	$54.1^{bB} \pm 9.5$	$43.2^{bAB} \pm 6.1$	$27.5^{cAB} \pm 1.4$	$10.6^{dAB} \pm 1.3$
	8	$14.0^{aC} \pm 0.6$	$36.2^{bcBC} \pm 11.2$	$32.4^{cAC} \pm 5.2$	$24.4^{bB} \pm 2.5$	$9.6^{dA} \pm 0.8$
	12	$10.5^{aD} \pm 1.0$	$21.8^{bC} \pm 6.6$	$23.6^{bC} \pm 7.0$	$18.1^{bC} \pm 1.1$	$9.4^{aAB} \pm 1.1$