

Litterfall and leaf decomposition in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina

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ABSTRACT: To achieve a fuller understanding of forest ecosystem functioning, it is necessary to know decomposition dynamics. The objective of this study was to quantify litter production, decomposition and mineralization in *Nothofagus pumilio* forests, in Tierra del Fuego, Argentina, along an altitudinal gradient during a two-year period and relate them to microclimate conditions and soil properties. We did the research along an altitudinal sequence at 210, 330, 460 and 590 m a.s.l., where climate, soil properties and forest structure were characterized. Litterfall decreased with altitude, and it was highly related with leaf and reproductive organ production. Decomposition decreased with altitude, being associated with microclimate and soil properties rather than with other measured variables, such as leaf chemistry. Values of decomposition constant (k) were influenced by altitude and varied between seasons and years within a given altitude. Nitrogen content increased with altitude in the two-year period, while P content decreased. Decomposition rates allowed us to separate the forest stands according to altitudinal gradients, and their intrinsic abiotic characteristics, which could increase the understanding of the nutrient flux and dynamics in these austral forest ecosystems.

Keywords: litter; microclimate; nitrogen; phosphorus

Litterfall from trees is one way of returning the nutrients contained in senescent plant organs (VOGT et al. 1986), representing the main flow of organic matter towards the forest floor (HERNANDEZ et al. 1992). The amount of litter production mainly depends on vegetation type, forest structure, climate and other environmental variables (BRAY, GORHAM 1964). This accumulated litter is reduced by physical degradation, heterotrophic consumption, and mainly by decomposition. Decomposition includes the chemical breakdown of litter, which transfers the organic matter and nutrients to the forest soil. This process is regulated by the interactions between litter quality, soil nutrients, climatic factors and decomposer organisms (SWIFT et al. 1979; AGREN, BOSATTA 1996; AERTS 1997). Litter quality influences the mineralization and immobilization processes (JARVIS et al. 1996), while temperature and moisture conditions affect the activity of the microorganisms which participate in decomposition (MARTIN et al. 1997).

Elevation gradients can serve as powerful experiments for studying how ecological processes are driven by changes in temperature and associated climatic variables, especially when other environmental factors are relatively constant (KORNER 2007; NORMAND et al. 2009). Changes in litter decomposability across gradients and thus temperature may help explain observed shifts in soil nutrient fluxes that have been found in several recent studies (HUBER et al. 2007; SOUNDQVIST et al. 2011).

Nothofagus pumilio (Poepp. et Endl.) Krasser, commonly called *lenga* in Spanish, is a deciduous species. It is a cold-tolerant species that occurs at lower (sea level) and higher elevations (tree-line) in southern Patagonia, constituting part of the world's most austral forests and reaching up to 55°S. Few studies have analysed decomposition in *Nothofagus* forests, as measured through litter weight losses. Existing studies have evaluated the interactions between microorganisms

and arthropods with leaf litter decomposition in laboratory conditions (GODEAS et al. 1985; COVARRUBIAS 1994); woody debris decomposition (CALDENTEY et al. 2001 FRANGI et al. 1997); the influence of forest management (CALDENTEY et al. 2001; IBARRA et al. 2011); and litterfall decomposition and cycling along an altitudinal gradient at the end of the year of incubation (BARRERA et al. 2000; FRANGI et al. 2005; DECKER, BOERNER 2006). However, for a holistic approach to the forest ecosystem functioning, it is necessary to know the dynamics of decomposition for longer periods, which will enable us to relate it with environmental variables. The objective of this work was to quantify fine litter production, leaf decomposition and mineralization in *Nothofagus pumilio* forests along an altitudinal gradient during two years, and relate them to microclimate conditions and soil properties.

MATERIAL AND METHODS

Study area. The study was conducted in Cerro Krund region (54°49'S, 68°42'W) located in the southern part of Tierra del Fuego Island (Argentina). Five sample sites were located on a south-facing slope and were established along an altitudinal gradient from the bottom of the valley to the tree-line: 210, 330, 460 and 590 m a.s.l.

The climate of the region is characterized by short, cold summers and long winters with snow and frost (TUHKANEN 1992), and it is classified in the sub-polar domain in the Southern Hemisphere (BURGOS 1985). Monthly mean air temperature ranged from ca -7 to 14°C. There are three months with mean temperatures below 0°C, growing season of about five months and precipitation near 600 mm per year in the valley. Soils have been described as Cryumbrepts, Cryohumods (GODAGNONE, IRISARRI 1990) and Spodic clayish soils (COLMET DAAGE et al. 1991). Upslope soils are characterized by a thin organic horizon overlying rock fragments while the mid- and down-slope soils are developed on sandy moraines. Upslope soils are more leached with lower base saturation than down-slope soils. Soils are usually shallow (B or B/C horizons commonly at 40–60 cm depth), with high phosphorus (P) content and frequent water retention in lower horizons. The parent material was till, composed of lutites containing mainly chlorite, illite and tephra (FREDERIKSEN 1988). Soils are generally acidic (3.3–5.2 water pH in organic and 3.2–4.0 in mineral horizons), with an effective cation exchange

capacity (ECEC) moderated in the organic levels ($> 25 \text{ cmol}(+)\cdot\text{kg}^{-1}$) and lower in the mineral horizons ($< 11 \text{ cmol}(+)\cdot\text{kg}^{-1}$) (NÓVOA MUÑOZ et al. 2006).

Forest structure. In each site, five plots were measured to describe the forest structure using a Criterion RD-1000 (Laser Technology, Place of producer, USA) with $K = 6$ (BITTERLICH 1984), determining the dominant height using an Impulse laser rangefinder (Laser Technology, Place of producer, USA), stand density, quadratic mean diameter and total over bark volume following the models proposed by MARTÍNEZ PASTUR et al. (2002).

Microclimate characterization. Four data loggers HOBO Onset were placed to monitor air and soil temperature at a depth of 15 cm. Each data logger was placed in a radiation shield at 150 cm under the overstorey canopy. Data were collected during the growing season from October 2003 to April 2004 and were analysed daily. Averages and standard deviations were obtained for each month in all the studied sites.

Soil properties. In the same plots used for the decomposition study, we sampled the forest floor and 0–10 cm of the mineral soil, in a track of 4 sub-plots. The subsamples were pooled in order to obtain one representative sample per plot. Air-dried soil samples were passed through a 2-mm sieve before the analyses: (i) pH in water (1:2.5), (ii) total soil N by semi-micro Kjeldahl, (iii) total organic C by dry combustion with an elemental analyser, and (iv) extractable P according to BRAY and KURTZ (1945). Five replicate samples of each plot were oven-dried (105°C) overnight to determine percent moisture in late spring (December), middle summer (February) and early autumn (April).

Litterfall. Fine litterfall was collected in five circular 0.5 m² traps area that were placed in five plots at each altitude. Samples were collected during leaf fall in 2003 and 2004. Litter from each trap was oven-dried at 60°C for 48 h. Dried samples were separated and weighed into four categories: leaves, small branches, seeds and miscellaneous material (lichens, reproductive organs, mosses, and remaining material).

Leaf decomposition and nutrient dynamics. In April during the autumn, recently abscised leaves were collected. This study concentrated on the analysis of leaf litter, because leaves are the main contributor to annual litterfall in *N. pumilio* forests (50–90% of the annual litterfall). Leaf material was air-dried until constant weight. Sub-samples from each altitude were weighed and oven-dried at 60°C for 48 h to calculate the initial moisture content of the leaf ma-

terial. Decomposition was analysed using the nylon mesh bag technique (BOCOCK et al. 1960). A total of 120 litter bags (4 altitude sites \times 6 collection dates \times 5 plots) with 3 g air-dried leaves in each (15 \times 15 cm with 2-mm mesh size) were placed in May before the beginning of winter on the forest floor at each altitude. Litter bags were fastened to the forest floor by metal pins to prevent movement and to ensure good contact between the litter bags and the organic layer. One litter bag per plot at each altitude was collected in 220, 300, 360, 600, 690 and 720 incubation days. Litter bags were cleaned to remove any exogenous material and weighed after oven-drying at 60°C for 48 h. Inorganic contaminants were quantified by the ashing of 0.5 g of leaf litter from each bag (500°C for 4 h) to correct the decomposition data obtaining. Initial leaf litter subsequent samples were analysed for N and P. Nitrogen was determined by semi-micro Kjeldahl and P according to the colorimetric technique (OLSEN, DEAN 1965; BREMNER, MULVANEY 1982). Mass loss and nitrogen and phosphorus release data were expressed as percentage of initial values on an ash-free basis.

Statistical analysis. Data were analysed by one-way or two-way analysis of variance (ANOVA) using Tukey's test to determine significant differences between mean values ($P < 0.05$). Decomposition rates were calculated using a single exponential decay Equation 1:

$$W_t = W_0 e^{-kt} \quad (1)$$

where:

W_t, W_0 – litter mass at time t and time 0,

k – decomposition constant (yr^{-1}),

t – time (yr) (OLSON 1963).

In order to correlate the mass loss after 720 days of incubation and the initial leaf litter quality parameters, and the soil properties and microclimate variables, Person's correlations were calculated. A comparison using a principal component analysis (PCA) for the plots at different altitudes using decomposition values obtained on the different sampling dates (220, 300, 360, 600, 690 and 720 incubation days) was done.

RESULTS

Forest structure

Forest structure of the sampled stands between 330 and 590 m a.s.l. corresponded to even-aged, pure old-growth forests, where no differences

in basal area were observed (32.0–52.8 $\text{m}^2 \cdot \text{ha}^{-1}$, $F = 2.4$ and $P = 0.107$). These stands presented crown covers up to 90%. Dominant height ($F = 210.7$ and $P = 0.001$), quadratic mean diameter ($F = 17.9$ and $P = 0.001$) and total over bark volume ($F = 6.7$ and $P = 0.004$) of the stands significantly diminished with altitude (20.1 to 5.7 m, 48.3 to 12.9 cm, and 521–188 $\text{m}^3 \cdot \text{ha}^{-1}$, respectively), while tree density ($F = 5.7$ and $P = 0.007$) significantly increased (900 to 4,000 trees $\cdot \text{ha}^{-1}$). At the valley floor (210 m a.s.l.), forests were composed of remnant old-growth trees mixed with a secondary forest established after logging that was carried out 50 years ago. The harvesting generated an uneven-aged structure with significantly lower values of the quadratic mean diameter than at the next higher altitude (32.7 cm compared to 48.3 cm). Dominant height was 19.9 m, tree density was 1,320 trees $\cdot \text{ha}^{-1}$, basal area was 49.6 $\text{m}^2 \cdot \text{ha}^{-1}$ and total over bark volume reached 473 $\text{m}^3 \cdot \text{ha}^{-1}$.

Microclimate characterization

Daily mean air temperature increased during the spring and reached a maximum during December (6.7–8.3°C). An increase in altitude corresponded with a decrease in the daily mean air temperature, where the range between the lower and the upper forest stands increased at the beginning of the spring, was highest during November (2.9°C between 210 and 590 m a.s.l.) and reached a minimum in the following months with a range of 0.7°C during April (Table 1). During this month, a thermal inversion was observed between 210 and 590 m a.s.l.

Daily mean temperature of soil at a depth of 15 cm was highest during February (5.1–6.0°C) and decreased with altitude with a range of 1.0°C to 1.8°C (Table 1). Thermal inversions were observed between 330 and 210 m a.s.l. from February to April, with a maximum range of 0.5°C.

Soil properties

Forest floor and mineral soil varied significantly between altitudes. The pH presented differences in the forest floor ($F = 58.1$, $P < 0.001$) and mineral soil ($F = 163.1$, $P < 0.001$), being higher at lower elevations (5.22 to 3.61 and 4.03 and 3.10 for 210 and 590 m a.s.l. for the forest floor and mineral soil, respectively). Extractable P also presented differences in the forest floor ($F = 28.2$, $P < 0.001$) and min-

Table 1. Microclimate of the studied altitude gradient

Factor (°C)	Altitude (m a.s.l.)	Daily mean (SD)						
		Oct	Nov	Dec	Jan	Feb	Mar	Apr
AT	210	2.4 (1.8)	5.2 (2.6)	8.3 (2.2)	6.7 (1.4)	7.7 (1.5)	5.6 (2.6)	3.9 (2.3)
	330	2.1 (1.8)	4.6 (2.7)	7.6 (2.2)	6.1 (1.4)	7.3 (1.6)	5.3 (2.6)	4.1 (2.4)
	460	1.5 (1.9)	3.8 (2.4)	7.0 (2.3)	5.5 (1.5)	6.6 (1.6)	4.7 (2.7)	3.6 (2.4)
	590	0.4 (1.9)	2.3 (2.5)	6.7 (2.4)	5.2 (1.7)	6.5 (1.9)	4.4 (3.0)	3.2 (2.8)
ST	210	1.6 (0.7)	3.6 (0.7)	5.6 (0.8)	5.8 (0.3)	6.0 (0.3)	5.3 (0.7)	4.5 (0.7)
	330	1.0 (0.6)	3.1 (1.0)	5.1 (0.9)	5.3 (0.3)	6.1 (0.4)	5.3 (0.9)	5.0 (0.5)
	460	0.5 (0.2)	2.1 (0.7)	4.3 (1.0)	4.8 (0.2)	5.2 (0.4)	4.4 (0.8)	3.7 (0.9)
	590	0.3 (0.1)	1.9 (1.4)	4.0 (0.8)	4.5 (0.2)	5.1 (0.3)	4.1 (0.8)	3.2 (0.8)

AT – daily mean air temperature, ST – daily mean soil temperature at a depth of 15 cm, Oct–Apr – month

eral soil ($F = 6.5$, $P = 0.004$), being higher at higher altitudes (51.7 to 152.3 ppm and 2.9 and 12.9 for 210 and 590 m a.s.l. for the forest floor and mineral soil, respectively). Total soil N varied significantly in the forest floor ($F = 15.4$, $P < 0.001$), being higher at middle altitudes (1.2–1.5% for 330–460 m a.s.l.) than at lower and higher altitudes (0.6–0.7%). Total organic C also varied significantly in the forest floor ($F = 143.8$, $P < 0.001$), increasing with altitude from 18.1 to 42.0%. As was observed for the two latter variables, the C/N ratio only varied significantly in the forest floor, being higher at higher altitudes, varying from 30.1 to 55.9.

Soil moisture varied between altitudes and time of sampling. At the beginning of the growing season (December) soil moisture was not significantly different ($F = 1.5$, $P = 0.254$, 23–38% soil moisture). During summer (February) soil moisture was significantly higher at lower altitudes ($F = 27.0$, $P < 0.001$, 86 to 45% for 210 and 590 m a.s.l., respectively). Finally, in early autumn (April) soil moisture increased signifi-

cantly with altitude ($F = 17.1$, $P < 0.001$, 9 to 31% for 210 and 590 m a.s.l., respectively).

Litterfall

Litterfall production varied significantly between years and elevations (Table 2). Total litter production was 1.4 fold greater during the first year than in the second year, mainly due to the higher amount of leaf material (2.0 t·ha⁻¹·yr⁻¹ compared to 1.0 t·ha⁻¹·yr⁻¹). Seeds and miscellaneous material (mainly composed of flowers and bud scales) were higher during the second sampling year than in the first year (0.17 compared to 0.09 t·ha⁻¹·yr⁻¹ and 0.23 compared to 0.08 t·ha⁻¹·yr⁻¹, respectively).

Total litterfall production was reduced with altitude (3.1 to 1.2 t·ha⁻¹·yr⁻¹), as well as the other studied components, with some inversions in the 330 m a.s.l. stands compared to 210 m a.s.l.

Table 2. Two-way ANOVA of the quantity of litterfall components in the studied period and along the altitude gradient

Main Factor		Litterfall (t·ha·yr ⁻¹)				
		leaves	branches	seeds	miscellaneous	total
Year	2003	2.022 ^b	0.399 ^a	0.093 ^a	0.078 ^a	2.593 ^b
	2004	1.049 ^a	0.387 ^a	0.174 ^b	0.233 ^b	1.845 ^a
Altitude (m a.s.l.)	210	2.099 ^c	0.688 ^c	0.199 ^c	0.159 ^b	3.146 ^c
	330	1.582 ^b	0.342 ^{ab}	0.133 ^b	0.208 ^b	2.265 ^b
	460	1.463 ^b	0.437 ^{bc}	0.160 ^{bc}	0.217 ^b	2.279 ^b
	590	0.999 ^a	0.107 ^a	0.041 ^a	0.038 ^a	1.185 ^a
F_{year}		172.1 ^{**}	0.1 ^{ns}	26.9 ^{**}	55.3 ^{**}	71.5 ^{**}
F_{altitude}		32.7 ^{**}	12.2 ^{**}	16.8 ^{**}	14.7 ^{**}	72.2 ^{**}
Interactions		29.2 ^{**}	4.6 [*]	6.1 ^{**}	4.1 [*]	35.0 ^{**}

F – Fisher test, *significant at $\alpha = 0.05$, **significant at $\alpha = 0.01$, ns – non-significant, ^{a–c} differences by Tukey's test at $\alpha = 0.05$

stands. Significant interactions were observed due to variations in the studied litterfall components between the extreme altitudes (210 and 590 m a.s.l.) (Table 2).

Decomposition and nutrient dynamics

The percentage of remaining leaf litter mass varied significantly through time and with elevation; but no interaction effect was detected for either factor (Table 3). The total percentage leaf litter loss was reduced with altitude, ranging from 52% at 210 m a.s.l. to 36% at 590 m a.s.l. after two years of incubation (Fig. 1). A greater leaf litter loss was measured during the first year of incubation (20–41% from low to high elevations). During the coldest months (mean air temperatures lower than 4–5°C, from May to November) a large loss of leaf material was observed. These losses were higher during the first year (11–29%) than in the second year (5–7%). During the warmest months (mean air temperatures higher than 4–5°C, from December to April) (Table 1), the losses were small but uniform along the altitudinal gradient. Decomposition during this period was similar during the first (9–12%) and the second year (5–13%).

Total k values after two years of incubation increased with decreasing elevation (0.22–0.37);

Table 3. Two-way ANOVA of decomposition and nutrient dynamics in the studied period and along the altitude gradient

Main Factor		Remaining mass	N	P
		(% of initial)		
Time (days)	220	81.71 ^f	101.97 ^a	56.36 ^a
	300	76.85 ^e	150.93 ^b	62.96 ^a
	360	71.26 ^d	152.27 ^b	71.85 ^{ab}
	600	65.14 ^c	178.04 ^c	83.08 ^b
	690	59.86 ^b	183.64 ^c	82.80 ^b
	720	55.24 ^a	192.72 ^c	85.53 ^b
Altitude (m a.s.l.)	210	58.03 ^a	161.06 ^{ab}	51.33 ^a
	330	64.83 ^b	147.55 ^a	71.02 ^b
	460	73.51 ^c	153.98 ^a	79.15 ^b
	590	77.00 ^d	177.11 ^b	93.56 ^c
F_{time}		155.8**	6.7**	38.8**
F_{altitude}		167.1**	30.6**	12.1**
Interactions		0.9 ^{ns}	0.01	0.001

F – Tukey's, *significant at $\alpha = 0.05$, **significant at $\alpha = 0.01$, ns – non-significant, ^{a–f} differences by Tukey's test at $\alpha = 0.05$

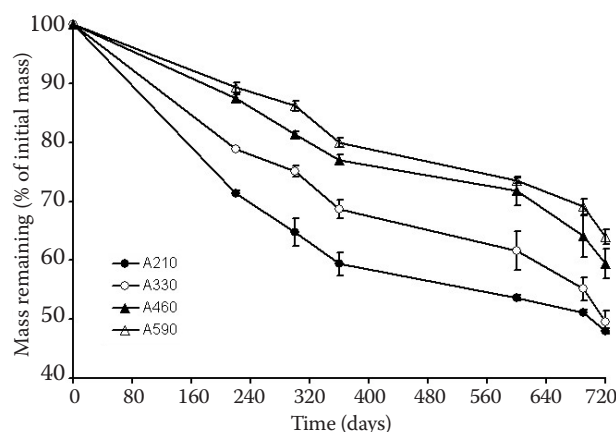


Fig. 1. Remaining mass of leaf litter (as percentage of initial mass) through time and altitude gradient. Means values of remaining mass are on ash-free basis \pm SE

maximum k values of 0.56, 0.40, 0.26 and 0.22 were recorded for each increasing altitude. At lower elevations (220 and 330 m a.s.l.), k was higher during the coldest months (0.56 and 0.40) than in the warmest months of the first year (0.46 and 0.35). This trend, however, was not observed at the upper altitudes (460 and 590 m a.s.l.), where k values were higher during the warmest months (0.32 and 0.28) compared to those of the coldest months (0.22 and 0.19). During the coldest months of the second year, lower k values were measured (0.12–0.18) than in the warmest previous and subsequent month periods (0.28, 0.54, 0.47 and 0.35 for 210, 330, 460 and 590 m a.s.l. stands, respectively).

The principal component analysis showed that axis one (eigenvalue = 5.151) was strongly related with altitude, while axis two (eigenvalue = 0.546) was related with the magnitude of decomposition (Fig. 2). Axis one explained 86% of the variance and all the sampling dates had the same importance, while axis two explained 9% of the variance and the importance of the variables increased with the time of incubation.

The percentage of leaf litter loss after 720 days of incubation and the initial N concentration were not correlated (0.620 $P = 0.796$), while the correlation was significant for litter

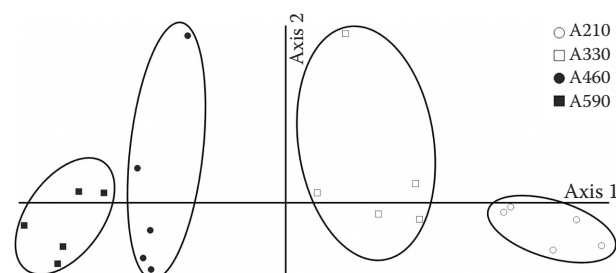


Fig. 2. PCA ordination based on the remaining mass through time at the studied altitudes

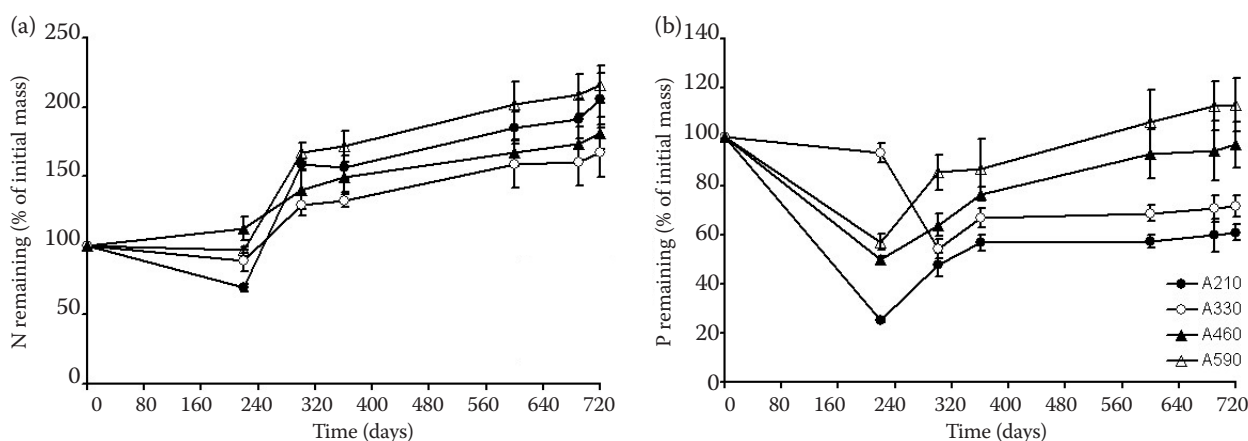


Fig. 3. Nutrient release from leaf litter during decomposition, expressed as percentage of initial nutrients, for (a) leaf litter N content and (b) leaf litter P content

loss and P content (-0.621 $P = 0.003$). Leaf litter N and P content significantly varied during the incubation time and with altitude, and interaction effects were observed (Table 3, Fig. 3). Nitrogen and P contents referred to the initial leaf litter mass, and increased during the two-year incubation (up to 190 and 85% for N and P). Nitrogen presented a net increase during the studied period, while P showed a decrease within 220 days and then slightly increased and remained constant for some sites or was higher than 100% (Fig. 3).

In the valley floor (210 m a.s.l.), a higher N was observed than in the middle of the hillside (330 m a.s.l.), and then increased again at higher altitudes (Table 3). When P was analyzed, a decrease was observed towards the bottom of the valley compared to higher altitudes, while a tendency towards an increase was detected near the tree-line (590 m a.s.l.).

Correlation of decomposition with soil properties, litter and microclimate

Leaf litter mass remaining after the full period of incubation was more closely related to microclimate and forest floor variables than to soil moisture or mineral soil. Mean soil temperature at a depth of 15 cm and daily mean minimum air temperature were negatively correlated with decomposition (-0.839 $P < 0.001$ and -0.479 $P = 0.017$, respectively). Total organic C (0.677 , $P = 0.001$), extractable P (0.698 $P < 0.001$), pH (-0.845 $P < 0.001$) and C/N (0.611 $P = 0.002$) were correlated with decomposition. Soil moisture was not significantly correlated with decomposition, while only in the mineral soil pH was significantly correlated (-0.746 $P < 0.001$) between the studied variables.

DISCUSSION

Litterfall changes between years and along an altitudinal gradient

Total litterfall values varied from 1.0 to $4.3 \text{ t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for the studied altitudinal gradient. The lower altitude presented differences associated with the forest structure generated by logging, while stands growing near the tree-line showed little variation between years. These values are comparable with those found by other authors in *Nothofagus* forests (BARRERA et al. 2000, CALDENTY et al. 2001), and by BRAY and GORHAM (1964) for cold temperate forests. CALDENTY et al. (2001) reported $2.0 \text{ t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in a primary unmanaged forest of *Nothofagus pumilio*, while BARRERA et al. (2000) described values ranging between 2.7 and $3.6 \text{ t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in an altitudinal gradient of *N. pumilio* from valley to tree-line. BRAY and GORHAM (1964) meanwhile reported values between 1.0 and $6.0 \text{ t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for cold temperate forests.

Leaves comprised the most important fraction of litterfall, as has been found for most of the forest ecosystems (LEBRET et al. 2001; LOWMAN 2001; SANTA REGINA, TARAZONA 2001). In this work, leaves represented between 50 and 94% of the total litter, with leaf production increasing near the tree-line (20–48%). However, BARRERA et al. (2000) described a lower percentage (68%) at the tree-line (640 m a.s.l.), compared to lower elevations (220–540 m a.s.l.) with values between 70% and 82% in a *Nothofagus pumilio* forest, while leaves accounted for 72% of the total litterfall according to CALDENTY et al. (2001). Leaves and reproductive parts showed a higher interannual variation. FERRARI and SUGITA (1996) suggested that the amount of reproductive organs leads to a reduc-

tion in leaf production, whereby energy taken for reproduction creates a deficit in the vegetative organs (LEBRET et al. 2001). Seeding cycles have been described in several forest species (KELLY 1994; KELLY et al. 2000; KOENIG, KNOPS 2000) and have received considerable attention in *Nothofagus* forests (MONK, KELLY 2006), because the level of variation between years is especially high (KELLY 1994; KELLY, SORK 2002). In this study, seed production and miscellaneous material, which mainly included reproductive organs, were higher at lower altitudes. In a seeding year, leaf production diminished to 50–57% compared to the non-seeding event year (71–78%). Besides this, the valley floor, which was harvested 50 years ago, presented changes in this pattern with a leaf production of 77% in the seeding year compared to 94% in the following year. This could be due to the fact that forestry intervention produced a significant effect on the annual litter flux, mainly on leaf mass production (ADU-BREDU et al. 1997; CALDENTEX et al. 2001).

Decomposition relationship with soil properties and moisture

Higher C/N ratios and lower pH values were related to the lower decomposition and mineralization rates of the organic material in the forest floor (STUMP, BINKLEY 1993). In our study, the decomposition rate decreased with altitude. The gradient in the pH values along altitudes was coincident with those values reported by DECKER and BOERNER (2003) in *N. pumilio* forests of Chile. Total organic C content was higher in the forest floor, which increased according to the altitude. The evident decrease in the decomposition rate of these forests with altitude explained the observed tendency of increasing organic C in the superficial forest floor levels, which was also described in similar studies (DECKER, BOERNER 2003; ROMANYÀ et al. 2005). N presented variable behaviour compared to C in the forest floor, although the increase with altitude did not greatly change. C and N contents in the mineral soil were lower than in the forest floor, and presented less variation with altitude. The C/N relationship increased with altitude, as was described by NÓVOA MUÑOZ et al. (2007). This fact suggests the importance of the organic horizons for nutrient recycling (VAN CLEVE et al. 1993).

P levels in the organic horizons are higher than those presented by GERDING and THIERS (2002) for *N. pumilio* and *N. betuloides* forests. Contents of available P in the forest floor are higher than those

found out in the mineral soil, which incremented with altitude. The magnitude of organic material accumulation is related with altitude, and can justify the tendency observed for P, which can be linked with the decrease of microbial activity (NÓVOA MUÑOZ et al. 2007). ROMANYÀ et al. (2005) and PEÑA RODRIGUEZ et al. (2013) described a close correlation between C and water soluble P contents in the organic horizons of *N. pumilio* forest soils.

Soil moisture in the forest floor is also closely related to decomposition rate, being one of the most frequently studied factors (e.g. PASTOR, POST 1986). In our study, the moisture levels presented differences between altitudes during summer and autumn, but were not correlated with decomposition rates, and therefore they are not a limiting factor for the decomposition process.

Decomposition along an altitudinal gradient

The pattern of decomposition found in this study agrees with most of the work presented for *Nothofagus pumilio*, where the percentage of mass loss is given mainly during the first year of incubation and does not change with altitude. Decomposition values were comparable to those reported by CALDENTEX et al. (2001) (59–80% of remnant mass) and GODEAS et al. (1985) (48–64% of remnant mass) in *Nothofagus pumilio* forests. CALDENTEX et al. (2001) results were obtained based on one year of field incubation, while GODEAS et al. (1985) determined it after one and two years in controlled laboratory conditions. The *k* values decreased when altitude increased, as was cited by BARRERA et al. (2000). The *k* values after one-year field incubation varied between 0.22 and 0.56, while BARRERA et al. (2000) found values of 0.40 to 0.79 for the altitudinal gradient. During the second year of field incubation the *k* values diminished their differences with values between 0.21 and 0.32. FRANGI and RICHTER (1994) published the *k* value of 0.56 for a *Nothofagus pumilio* stand at 220 m a.s.l. in Tierra del Fuego, while DECKER and BOERNER (2006) reported *k* values of 0.23 in Central Chile and BAHAMONDE et al. (2012) between 0.20 and 0.30 for *Nothofagus antarctica*.

Decomposition could be related to chemical tissue content, microclimatic conditions, soil properties and soil organism activity. BARRERA et al. (2000) suggested that N content could influence decomposition. In our study N content of the leaf litter did not significantly vary. As a result, it is expected that decomposition could be better explained by

the other factors. Decreases in the decomposition rate with increasing elevation appeared therefore to be related to differences in microclimatic conditions (COUTEAUX et al. 1995; BARRERA et al. 2000), with few exceptions (e.g. HOBIE, CHAPIN 1996), whereby the mass loss resulted from biological activity during winter or due to physical processes (e.g. fragmentation or leaching). In this study, the physical decomposition during winter was decreasing with altitude and reached the values of 29 to 11% from 210 to 590 m a.s.l. KURKA et al. (2000) found positive correlations between leaf litter decomposition and air temperature and soil moisture whereas in this study significant correlations with air and soil temperatures were found for decomposition rate, while soil moisture was not related. In other studies soil moisture even overrode the importance of temperature. In an altitudinal gradient, MURPHY et al. (1998) reported greater decomposition rates at higher, colder and wetter sites compared with low, warmer and drier ones. This last study also clearly showed the interplay of temperature and moisture, and corroborated the conclusion that litter decomposition rates will increase only in warmer conditions if soil moisture is sufficiently high (AERTS 2006).

PCA correctly separated the plots according to their altitude, where groups remained orderly according to Axis 1. This indicated that environmental changes derived from altitude controlled the decomposition rate, as well as the forest structure and their specific communities, as previously reported (MARTÍNEZ PASTUR et al. 1994). The main changes are related to microclimatic conditions that affect soil properties and soil organism activity. On the other hand, plots at the extreme altitudes (210 and 590 m a.s.l.) are more homogeneous, while the intermediate ones presented a higher dispersion (Axis 2). This could be due to the climatic conditions in the valley bottom (thermal inversion effect) and near the tree-line they are more stable than at the mid-slope (MASSACCESI et al. 2008).

The *k* values were found to vary between seasons, being higher during summer-autumn than in winter-spring, which could be related to temperatures and microorganism activity. Besides this, decomposition was higher during the first winter at low altitudes (220–360 m a.s.l.) (0.40–0.56 in winter-spring compared to 0.35–0.46 in summer-autumn). Decomposition during winter-spring could be due to a mechanical break of the litter (TAYLOR, PARKINSON 1988; HOBIE, CHAPIN 1996) or due to fungi decomposition (GODEAS et al. 1985), and also due to a rapid degradation of the more labile leaf

compounds, such as soluble carbohydrates, during the initial phases of decomposition (SUBERKROPP et al. 1976). Another climate phenomenon that could influence decomposition was the characteristic inversion of air and soil temperatures that occurred at the valley floor (PEROYVIND 1990), as was previously presented.

Mineralization and immobilization

The expression of the N and P contents of the leaf litter bags as a percentage of the initial content allowed for the determination of net N and P dynamics (SANTA REGINA et al. 1997). In case that tissues accumulate nutrients over time (e.g. > 100% N or P), this reflects nutrient gain by immobilization, N-fixation, or atmospheric deposition. An immobilization of the N content was observed along the two-year period of observations, except at the lower altitudes during the first winter-spring seasons. Several studies on litter decomposition showed an increase in N content related to litter mass losses (BERENDESE et al. 1989; BALLINI, BONIN 1995). Several processes have been proposed to explain N accumulation through inputs by leaching from canopy, atmospheric N fixing, fungal and bacterial development, soil fauna excrements or N contamination with organic matter (VAN VUUREN et al. 1993; SANTA REGINA et al. 1997). This phenomenon could be explained by microorganism immobilization due to the scarce N soil availability which was evident from the C/N ratios (NÓVOA MUÑOZ et al. 2007).

Contrary to the N dynamics, P litter content mainly presented mineralization. At lower altitudes higher mineralization values were observed, while at higher altitudes lower mineralization was observed reaching immobilization values at the end of the study. During the first year of decomposition, the strong mineralization could be explained by the leaching of the more labile compounds. The immobilization of P occurred when the decomposition rate was relatively low, which suggests that accumulation was not only caused by microbial immobilization. Mechanisms such as translocation of P from fungal hyphae (AERTS, CHAPIN 2000) may have occurred, where *N. pumilio* forest presented large fungi biomass and diversity (GODEAS et al. 1985).

Overall, there was a large difference between the P and N dynamics in the leaf litter. The initial net mineralization of P was much greater than that of N, suggesting that N is more important than P as a control of initial leaf litter decay. The N/P ratio varied between 3.9 and 5.2 for leaf litter. This implies that these sub-

strates may have a relative shortage of N for decomposers, because the N/P ratio in bacterial and fungal cells is in the range of 10–15 (SWIFT et al. 1979).

CONCLUSIONS

Litterfall quantity decreased with altitude, and leaf and reproductive organ production were highly related in *Nothofagus pumilio* forests. Leaf production was variable between years, being more stable near the tree-line. Decomposition decreased with altitude and was more related to microclimate and soil properties than to other factors. This long-term decomposition study allowed us to understand nutrient cycle balances in the stands, which explained the higher accumulation values found in the forest soils and the influence of mechanical decomposition in the whole process. N content was mainly immobilized, while P content was mainly mineralized, being higher with altitude in the two-year period. Finally, decomposition rates allowed us to separate the stands according to the elevation gradient and their intrinsic abiotic characteristics (soil properties and microclimate), which could increase the understanding of the nutrient flux dynamics in the world's southernmost forested ecosystems.

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