# Leaf litter breakdown in Patagonian streams: native versus exotic trees and the effect of invertebrate size

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ABSTRACT

1. *Nothofagus* native forest in the Southern Andes is being progressively substituted by forestation with rapid growth of the exotic trees, mainly species of Pinaceae. The effect on stream processing dynamics is explored through in situ experiments.

2. The effects of leaf litter quality and macroinvertebrate size on *in situ* litter breakdown were analysed. Experiments were run in litter bags which allowed access of macroinvertebrate fauna in streams running through a dense forest of the deciduous *Nothofagus pumilio*.

3. In Experiment 1, the decay rates of *N. pumilio* leaves and *Pinus ponderosa* needles were measured during an autumn-winter period. *N. pumilio* decayed twice as fast as *P. ponderosa* ($P < 0.01$). Shredders fed only on *N. pumilio* leaves. The total abundance of macroinvertebrates colonizing both treatments was similar; however, the biomass was higher in the *N. pumilio* treatment. Large shredders were only found colonizing *N. pumilio* leaves. Since no decay due to shredders was observed in *P. ponderosa*, the presence of macroinvertebrates in these litter bags was related to refuge and feeding on FPOM-biofilm resources.

4. In Experiment 2, *N. pumilio* leaf litter was exposed in order to allow (open bags) or restrict (closed bags) access of invertebrates. The invertebrate assemblage in open bags showed the similar pattern observed for *N. pumilio* in the first experiment. Gathering-collectors were generally smaller and dominant in number while shredder biomass was higher in open bags as a result of high individual biomass. *N. pumilio* decayed faster when the whole size spectrum of macroinvertebrates colonized the bags ($P < 0.01$). However, feeding signs of small shredders were observed in closed bags, therefore their role on leaf litter breakdown in Andean streams should not be neglected.

5. The combined results of both experiments lead to the conclusion that the whole litter processing mechanism would be affected as a consequence of the substitution of native forest by exotic pine forestation. Copyright © 2002 John Wiley & Sons, Ltd.

KEY WORDS: litter decay; streams; deciduous *Nothofagus pumilio*; shredders; Andes; *Pinus ponderosa*

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# 1. INTRODUCTION

Native forests in Patagonia cover the headwaters of all the Pacific and Atlantic basins. They extend on both sides of the western Andes range between 39°S and 55°S. As in other areas of the world, land use has gradually changed the native woodland. Agriculture, and wood extraction for heating for the paper and construction industries have been important historically mainly in the Western Andes (Chile) (Donoso and Lara, 1996). However, forestry has become increasingly relevant from the 1950s, particularly by the replacement of woodland with rapid growth species such as pines and eucalyptus (Lara *et al.*, 1996). The Pacific native forests have been severely altered, reaching up to 60% of woodland substitution with monocultures of exotic species in several regions of Southern Chile between 1978 and 1987 (Lara *et al.*, 1996). On the other hand, the Atlantic slope, with about 2,600 km$^2$ of native woodland, has suffered considerably less impact. In Argentina, however, forestry is promoted and grant-aided by the Federal Government of Argentina (Postler *et al.*, 1999). Up to 1998, the Andes eastern slope (Argentina) was forested with about 500 km$^2$ of pine plantations and it was estimated that this would reach about 800 km$^2$ at the present (Schlichter and Laclau, 1998). Including both the Andean (woodland) and the extra-Andean (ecotone woodland-steppe) areas of Argentina, these authors mentioned that between 7000 and 20 000 km$^2$ are suitable for pine introduction.

Forest substitution in the Andes of Patagonia has mainly produced ecological consequences in the same terrestrial ecosystem, such as lowering biodiversity both of plants and vertebrates (Lara *et al.*, 1996; Murúa, 1996; Rozzi *et al.*, 1996). Because riparian vegetation is linked to instream processes, it is expected that its alteration cause changes in aquatic systems (Cummins *et al.*, 1989). These changes may influence food resources for stream communities by altering the input timing, standing crop or food quality of detritus (Sedell *et al.*, Cummins *et al.*, 1989; Murphy and Giller, 2000). Thus, it has been suggested that debris processing in streams has been affected by the introduction of *Eucalyptus* in Portugal (Abelho and Graca, 1996) and by extensive plantations of *Pinus radiata* in Australia (Campbell, 1994). In-low order forested streams, allochthonous organic matter is a major source of food and refuge for aquatic invertebrates (Smock *et al.*, 1989; Prochazka *et al.*, 1991; Dobson, 1994). Invertebrates inhabiting these organic patches are mainly detritivores belonging to the shredder and gathering-collector guilds (Cummins *et al.*, 1989) and both groups are predicted to coexist in headwaters (Vannote *et al.*, 1980). Biological processes may account for up to 70% loss in leaf litter mass in a stream patch (Cummins, 1996) with shredder feeding activity as a significant contributory factor (Petersen and Cummins, 1974; Cuffney *et al.*, 1990; Stewart, 1992; Robinson *et al.*, 1998). Coarse detritus-feeders are generally large invertebrates adapted to shred and feed on large plant debris. However, smaller invertebrates may also be important in the breakdown of coarse particulate organic matter (CPOM) (Short *et al.*, 1980; Graça *et al.*, 1993; Dieterich and Anderson, 1995).

In Andean canopied headwaters, the *Nothofagus* temperate forest is the most important source of organic matter (Modenutti *et al.*, 1998). The genus *Nothofagus* is endemic to the Southern Hemisphere (Allan, 1982) and deciduous species are restricted to South America, where six tree species develop in the temperate forests. Among these, *N. pumilio* has the broadest distribution, from 39° to 55°S forming a low temperature treeline at higher elevations (Barrera *et al.*, 2000), a feature indicated as distinctive of the Southern Andes (Wardle, 1998). Until now, *Nothofagus* decay has only been studied in New Zealand evergreen tree species (Davis and Winterbourn, 1977; Rounick and Winterbourn, 1983; Linklater, 1995) and recently in Southern Argentina (Albariño and Balseiro, 1998, 2001). Over the last 30 years, exotic species of Pinaceae have been introduced into the Atlantic slope of the Southern Andes (Schlichter and Laclau, 1998). However, the impact of such activity on aquatic systems has not yet been evaluated. Although Fagaceae have been reported to have very low decay rates, Pinaceae attain the lowest known values (Webster and Benfield, 1986). Therefore, substitution of native woodlands with Pinaceae forest would affect instream benthic CPOM-dynamics by altering both trophic assemblages and litter decay rates, since shredders would be less able to process such new debris.

Using in situ experiments, this study attempts to analyse the effect of substituting *Nothofagus pumilio* litter by *Pinus ponderosa* needles in low order South Andes streams. A subsequent experiment explores the effect of excluding large shredders on *Nothofagus pumilio* leaf litter decay.

## STUDY AREA

The experiments were carried out in the upper section of the Ñireco catchment ($41°08'S$; $71°17'W$). This basin drains an area densely covered by a forest of *N. pumilio* (called 'lenga') a species of deciduous beech that dominates the vegetation and forms the highest mountain belt of the temperate forest up to the timberline in the Patagonian Andes. The basin has a pluvio-nival hydrological regime with high discharge in autumn (rain) and spring (snowmelt) and low discharge in late summer. Ñireco stream discharges range from $2300 \, L/s^{-1}$ (mean maximum — November) to $230 \, L/s^{-1}$ (mean minimum — March).

Two different experiments were carried out, Experiment 1 in the main channel of Ñireco stream and Experiment 2 in an unnamed tributary called hereafter A1. Experiments were performed in riffle areas of both streams where the substrate was dominated by boulders and cobbles. Chemical characteristics were similar: conductivity $48.8 \, \mu S \, cm^{-1}$, pH neutral to slightly basic (7.7), and dissolved oxygen concentration always at saturation levels. The main differences between both streams are order and width since Ñireco stream is a second-order stream and 4 m wide, while A1 is a first-order stream and 1 m wide.

## MATERIALS AND METHODS

### Experiment 1

This experiment was conducted in Ñireco stream during autumn–winter 1995. Litter bags were used to measure processing rates and macroinvertebrate colonization for leaf litter of both a native and an exotic tree species. *Nothofagus pumilio* leaves range from 20 to 40 mm in length and bags are more adequate than other methods when used with small leaves (Davis and Winterbourn, 1977). Litter bags of $18 \times 12 \times 2 \, cm$ were constructed combining two mesh sizes 10 mm (15% of bag surface) and 1 mm (remaining 85%) — and placed in the substrate with the large mesh size upstream. Thus, it was assumed that large macroinvertebrates could gain access to leaves and also that leaf fragments ($>1 \, mm$) produced by the breakdown processes would not be washed out. Physical abrasion was assumed to be negligible because of the physical protection provided by bags. Therefore, the loss of leaf mass inside the bags was attributed only to leaching, microbial decomposition and macroinvertebrate activities. Undamaged freshly fallen leaves of *N. pumilio* were collected from the riparian zone, and needles of *P. ponderosa* were obtained from a pine plantation nearby, both collections being made on 14 May 1995 (Southern autumn). Two treatments were performed: one with *N. pumilio* leaves (Np) and another with *P. ponderosa* needles (Pp). Each bag was filled with fresh leaves of one species equivalent to 4.00 g DM (dry mass) weighed to the nearest 0.01 g. The amount of leaf litter was 50% greater than the estimated CPOM mass $m^{-2}$ for this stream (R. Albariño, personal observation). Leaves used in experiments were not artificially dried to avoid overestimation of decay rates (Gessner and Dobson, 1993). Leaf dry mass in the mesh bags was estimated by the following regressions:

$$DM_{Np1} = 0.50 \, FM_{Np1} + 0.19 \, (r^2_{adj} = 0.99, \, n = 14)$$

$$DM_{Pp} = 0.84 FM_{Pp} + 0.03 (r^2_{adj} = 0.99, \, n = 14)$$

where FM is the fresh mass of leaf or needle. Dry mass was determined by drying leaf material at 60°C for 48 h and weighing to the nearest 0.01 g. During that time, fresh leaves were stored in a refrigerator at 5°C in dark conditions. Stored leaves lost about 5% of their initial fresh mass (probably due to water loss) and this factor was included in the estimation of fresh mass in the bags.

On 17 May 1995 ($t_0$), 20 bags of each leaf species were introduced in an 80 m-reach of Ñireco stream. Each bag was ballasted with a small cobble inside and placed randomly in one of four riffle areas. Five bags (i.e. five replicates) of each treatment were removed after 2, 16, 42 and 118 days of exposure ($t_2$, $t_{16}$, $t_{42}$ and $t_{118}$) and returned to the laboratory.

In the laboratory, macroinvertebrates were separated from remaining leaf material by rinsing. Leaf remaining dry mass (LRDM) for each bag was obtained by drying at 60°C for 48 h. Macroinvertebrates were taxonomically identified and assigned to their corresponding functional feeding groups (FFGs) according to Merritt and Cummins (1996): shredder, gathering-collector, filtering-collector, scraper and predator. Taxa were assigned to each FFG by a combination of methods (mouthpart morphology, gut content analysis and/or feeding experiments) (Albariño and Valverde, 1998; Albariño, 1999; Díaz Villanueva and Albariño, 1999; Albariño, 2001). Some taxa were assigned using the classification of Merritt and Cummins (1996) and related literature. In the present analysis only detritivore groups associated with leaf litter — shredders and gathering-collectors — were considered. Following Cummins and Merritt (1996), early instars of shredders were assumed to be gathering-collectors. Macroinvertebrates were quantified both in number and biomass and relative values were referred to as grams of LRDM for each experimental unit. Biomass was obtained by drying organisms at 60°C for 24 h and weighing to the nearest 0.01 mg.

An exponential decay model was estimated in both treatments for LRDM versus time:

$$W_t = W_0 e^{-kt}$$

where $W_t$ is the LRDM at a given time $t$, $W_0$ is the initial leaf DM, $k$ is the decay rate and $t$ is time in days. Based on this model $t_{50\%}$ was calculated, i.e. the time when the first 50% of CPOM would decay.

## Experiment 2

This experiment was conducted in stream A1 during spring–summer 1995–1996. Similar bags to those in Experiment 1 were used in two treatments in order to test the effect of shredder size on leaf litter breakdown of *N. pumilio*. The open bag treatment (OB) consisted of composite bags as in Experiment 1, which allowed large shredders to colonize. Closed bag treatment (CB) consisted of similar plastic bags but constructed entirely of 1 mm mesh to restrict the access of large invertebrates.

*N. pumilio* leaves were collected from stream surroundings on 13 November 1995; therefore they had overwintered on the ground during the rainy and snowy period. Each bag of both treatments was filled with the equivalent of 3.50 g DM of leaves, and then ballasted with a cobble. Dry mass of leaf material was estimated by the following regression equation established using the same procedure as in Experiment 1:

$$DM_{Np2} = 0.87\, FM_{Np2} \text{-} 0.02 (r^2_{adj} = 0.99, n = 12)$$

Thirty bags of OB and 15 of CB were placed in the stream on 17 November 1995 ($t_0$). Five bags (i.e. five replicates) of OB were removed at 7, 20, 32, 47, 89 and 135 days, and five bags of CB (replicates) were removed after 20, 47 and 135 days of exposure. The same procedure of Experiment 1 was followed to obtain LRDM, number and biomass of macroinvertebrates from each experimental unit. An exponential model for each treatment was estimated for LRDM versus. time and $t_{50\%}$ was calculated.

In order to test for statistical differences in decay rates ($k$) between treatments in each experiment, leaf dry mass data were log-transformed and a regression model against time was obtained. Regression coefficients were compared using the method of Sokal and Rohlf (1981) and difference was tested at 1% significance.

## RESULTS

### Experiment 1

Water temperature was 3.4°C ($\pm$ 0.4; mean $\pm$ SE). Maximum and minimum temperatures were 4.5°C (May) and 1.0°C (June), respectively. At day 2, mass loss due to leaching was 3.8% for *N. pumilio* and was not detectable for *P. ponderosa*. Feeding signs by macroinvertebrates were observed on *N. pumilio* leaves at $t_{42}$ indicating that feeding activity had started after $t_{16}$. In contrast, needles showed no evidence of having been fed on throughout the experiment. The decay rate coefficient ($k$) of *N. pumilio* was significantly higher than that of *P. ponderosa* ($P < 0.01$) (Table 1, Figure 1(a)). The estimated $t_{50\%}$ for *P. ponderosa* was twice that of *N. pumilio* leaves (Table 1). At day 118, leaves and needles had lost 34% and 19% of their initial DM (Figure 1(a)). Although bags were placed with the large mesh size upstream, no coarse litter, not included originally in the bags, was found; this was especially evident in the pine bags, where any other litter can be easily recognized.

Macroinvertebrates gradually colonized the litter bags and maximum mean densities (49 and 56 ind. g$^{-1}$ LRDM for Np and Pp, respectively) were registered at day 118 (Figure 1(b)). However, macroinvertebrate biomass was higher at day 42 for Np (7.4 mg DM ind. g$^{-1}$ LRDM) and at day 118 for Pp (5.1 mg DM ind. g$^{-1}$ LRDM) (Figure 1(c)). Shredders colonized both treatments in a similar numerical pattern, corresponding to 5% and 10% of total macroinvertebrates in Np and Pp, respectively. Shredders were mainly represented by larvae of three plecopteran families: Austroperlidae (*K. kuscheli*), Gripopterygidae (*Antarctoperla michaelseni* (Klapalek)), Notonemouridae (*Austronemoura* sp. and *Udamocercia uramifera* (Aubert)), and one trichopteran family: Sericostomatidae (*Parasericostoma cristatum* Flint). Although the shredder density was around 1 ind. g$^{-1}$ of LRDM in both treatments (Figure 1(d)), the biomass showed a different pattern. In Np, shredder biomass represented up to 53–83% of total macroinvertebrate biomass ($t_{42}$–$t_{16}$, respectively). Maximum biomass was 3.9 mg g$^{-1}$ LRDM at $t_{42}$ (53%). In Pp, shredder biomass was considerably lower than in the other treatment, ranging from 0.2 to 1.0 mg g$^{-1}$ LRDM ($t_2$–$t_{118}$) accounting for 19% of total macroinvertebrate biomass. During the experiment, gathering-collectors increased both in number and biomass (Figure 1(f) and (g)) in both treatments. In terms of density, they represented the major component of the macroinvertebrate assemblage (Figure 1(b)–(f)), since a large number of oligochaetes, chironomids and ephemeropterans colonized the bags. The relative abundance of gathering-collectors to total macroinvertebrates ranged from 83% to 88% (Np) and 62% to 87% (Pp). In terms of biomass, this fraction ranged from 9% to 35% (Np) and from 19% to 35% (Pp).

Table 1. Breakdown estimates of leaf litter for the two experiments in Ñireco basin

| Treatment | Stream temperature (°C) | Decay rate (d$^{-1}$) $\pm$ SE | $t_{50\%}$ (d)[a] | $N$ | $r^2_{adj}$ | $F_s$[b] | df | $F_{\alpha\ 0.01}$[b] |
|---|---|---|---|---|---|---|---|---|
| **Experiment 1** | | | | | | | | $F_{(1,\ 30)}$ |
| *Nothofagus pumilio* | | 0.0033 $\pm$ 0.0003 | 212 | 20 | 0.90 | | | |
| | 1.0–4.5 | | | | | 21.53 | 36 | 7.56 |
| *Pinus ponderosa* | | 0.0017 $\pm$ 0.0002 | 408 | 20 | 0.78 | | | |
| | | | | | | | | |
| **Experiment 2[c]** | | | | | | | | $F_{(1,\ 40)}$ |
| Open bags | | 0.0074 $\pm$ 0.0007 | 94 | 30 | 0.89 | | | |
| | 5.5–13.5 | | | | | 21.15 | 41 | 7.31 |
| Closed bags | | 0.0053 $\pm$ 0.0001 | 131 | 15 | 0.99 | | | |

[a] $t_{50\%}$ is the time when the first 50% of CPOM would decay.
[b] $F_s$ and $F_{\alpha\ 0.01}$ — statistic and critical values for the regression coefficient's comparison method.
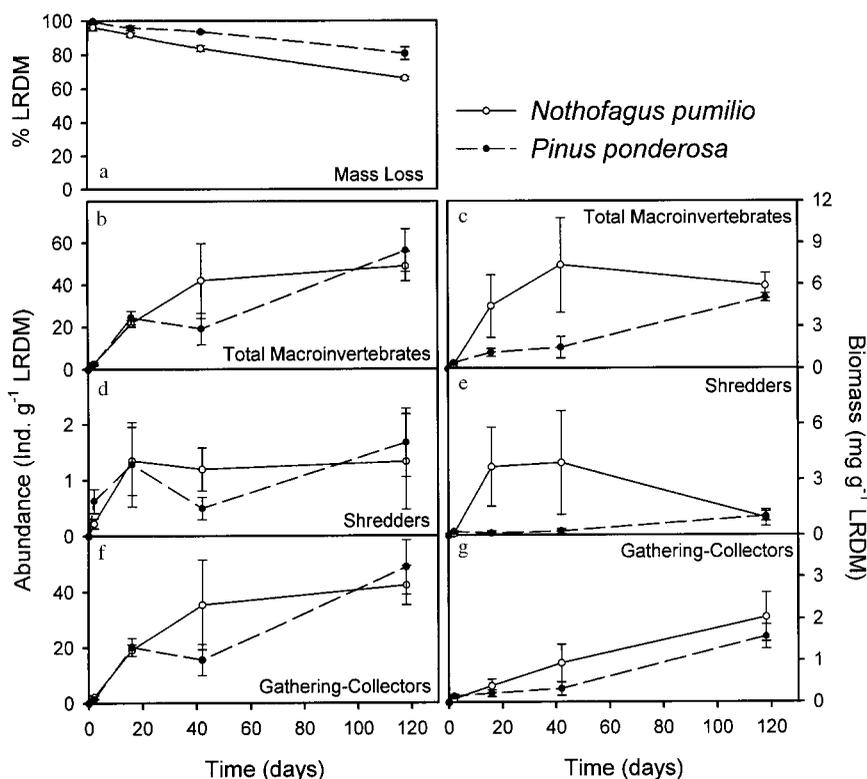[c] conducted with *N. pumilio* leaves.

Figure 1. Leaf litter mass loss and macroinvertebrate colonization for *Nothofagus pumilio* and *Pinus ponderosa* treatments (Experiment 1). LRDM = leaf remaining dry mass ± 1 SE.

Individual mean biomass of shredders was always higher than that of gathering-collectors in both treatments (Figure 2(a)). Shredders colonizing Np presented the highest individual mean biomass, with maximum values at $t_{16}$ and $t_{42}$ (about 3 mg ind.$^{-1}$). Gathering-collector individual biomass was rather constant throughout the experiment, and it slightly increased towards the end of the experiment (0.1 mg ind$^{-1}$ at $t_{118}$) (Figure 2(a)).

**Experiment 2**

Mean water temperature was 8.7°C. (± 0.8 SE). Lower temperatures were recorded in November (5.5°C) and March (7.5°C) while higher ones were measured in December (13.5°C). During the first 7 days, mass loss, only measured in open bags, accounted for 6% of initial leaf litter. Subsequently, leaf fragmentation gradually increased towards the end of the experiment. Although this process was apparently higher in open bags, shredder feeding signs on leaves were also identified in closed bags. At day 135, leaf material had lost 69% (OB) and 51% (CB) of their initial DM (Figure 3(a)).

Decay rate of *N. pumilio* leaves was significantly higher in OB than in CB ($P < 0.01$) (Table 1, Figure 3(a)). The estimated $t_{50\%}$ in OB treatment was almost one half of that for CB (Table 1).

Total macroinvertebrate abundance showed an increase towards the end of the experiment (Figure 3(b)) with a maximum of 322 ind. g$^{-1}$ LRDM in open bags and 97 ind. g$^{-1}$ LRDM in closed ones. Biomass was markedly higher in OB, ranging from 18.6 to 38.8 mg g$^{-1}$ LRDM (Figure 3(c)), while in CB it ranged from 1.4 to 7.1 mg g$^{-1}$ LRDM. The closed treatment successfully prevented the access of large
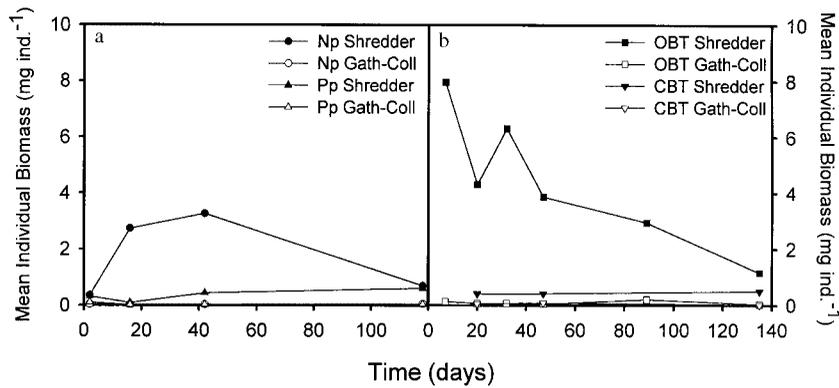
Figure 2. Individual biomass of shredders and gathering-collectors colonizing leaf bags in Experiment 1 (a) and Experiment 2 (b). Np = *N. pumilio*, Pp = *Pinus ponderosa*, OBT = open bag treatment and CBT = closed bag treatment. Mean ± 1 SE.
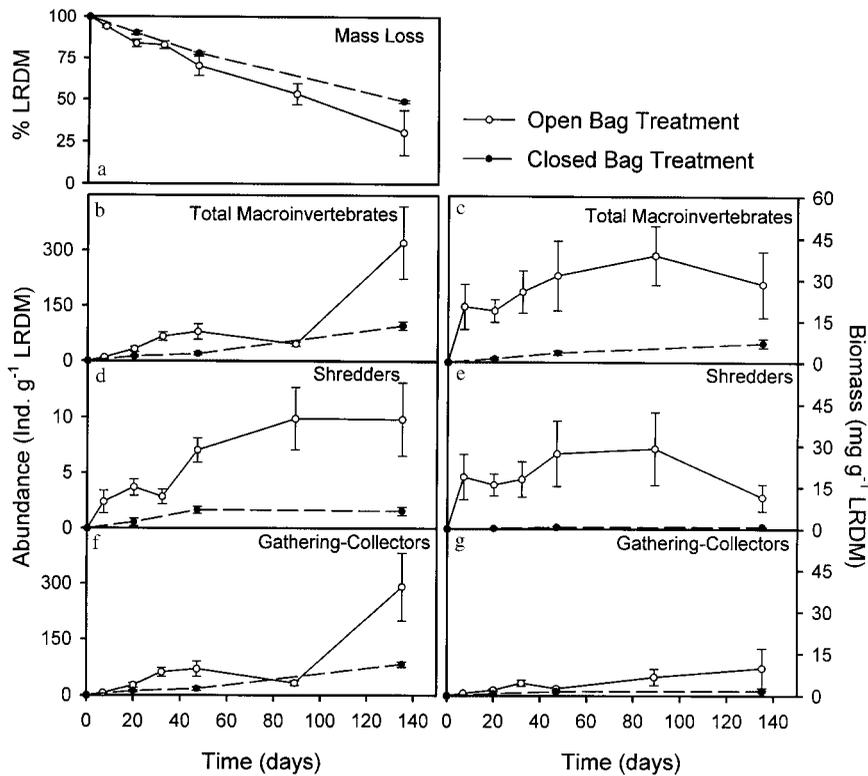


Figure 3. Mass loss and macroinvertebrate colonization of *Nothofagus pumilio* leaf litter for open and closed bag treatments (Experiment 2). LRDM = leaf remaining dry mass ± 1 SE.

macroinvertebrates to the leaf litter inside the bags. This difference was observed for both shredders and gathering-collectors, in terms of abundance and biomass (Figure 3(b)–(g)).

Shredders represented by Plecoptera, Diptera and Trichoptera larvae colonized both treatments, but they were more abundant in OB (7–10 ind. g$^{-1}$ LRDM) (Figure 3(d)). In open bags, shredder biomass increased

to 29.2 mg g$^{-1}$ LRDM at day 89, when litter had lost 47% of its initial dry mass (Figure 3(e)). In closed bag treatments, shredder density and biomass showed a tendency to increase. At day 135, both values were 2.0 ind. g$^{-1}$ LRDM and 0.8 mg g$^{-1}$ LRDM respectively (Figure 3(d) and (e)). Although in open bags, the relative density of shredders to total macroinvertebrates was low (3–25%), in terms of biomass they accounted for 70–93%, except at $t_{135}$ when they decreased to 40%. Mean individual biomass of shredders decreased substantially during the experiment from 8.0 ($t_7$) to 1.1 mg ind.$^{-1}$ ($t_{135}$) in OB (Figure 2(b)). In closed treatments, lower values were found throughout the experiment, up to 0.5 mg ind.$^{-1}$ (Figure 2(b)). In contrast to the pattern registered in OB, mean biomass per shredder increased 18% in CB. Large shredders (intermediate and large-sized instars of *K. kuscheli*, trichopteran *Monocosmoecus* sp., and the dipteran *Tipula* sp.) only colonized the open bags. On the other hand, closed bags were colonized by small shredders such as the plecopteran *Antarctoperla michaelseni* and *Parasericostoma cristatum*, corresponding with the presence of shredding signs on leaves. Many leaves were found shredded and leaf fragmentation increased remarkably throughout the experiment as in open bags, indicating that smaller invertebrates were able to bring about loss in CPOM mass.

Gathering-collectors were represented by Oligochaeta, Ephemeroptera, Diptera and early instars of shredder taxa. In open bags, abundance increased throughout the experiment, reaching 291 ind. g$^{-1}$ LRDM (Figure 3(f)), although a slight decrease at day 89 was observed (Figure 3(f)). The relative abundance of gathering-collectors was always high, varying between 63% and 92% in open bags and 85% and 87% in closed ones. Individual mean biomass was always low in both treatments (Figure 2(b)). Due to their smaller size, the contribution to total biomass was low (4–35% of total macroinvertebrates) in spite of their high densities. The mesh size also limited the access of this feeding group, since density and biomass were lower in closed than in open bags (Figure 3(f) and (g)).

## DISCUSSION

In the autumn-winter experiment (Experiment 1), both CPOM decay rate and invertebrate colonization differed between the two treatments (Figure 1). Although the native *Nothofagus pumilio* and the exotic *Pinus ponderosa* litter showed very low leaching, *N. pumilio* leaves were eaten by shredders and decayed faster than *P. ponderosa* needles. Conifer needles have highly refractory organic compounds (Sedell *et al.*, 1975; Gregory *et al.*, 1991) and Pinaceae have the lowest decay rates known (Webster and Benfield, 1986). Cuticular thickness and presence of resins delay microbial conditioning and thus its availability for detritivores (Bärlocher *et al.*, 1978; Michaelides and Kendrick, 1978). In another study with litter 1 month pre-conditioned, Albariño and Balseiro (2001) found *P. ponderosa* leaf toughness to be nine times higher than that of *N. pumilio* leaves. Fagaceae also have low decay rates (Webster and Benfield, 1986) and *N. pumilio* mass loss obtained in the winter experiment (3.4°C, mean temperature) was 34% after 118 days. However, *P. ponderosa* decay rate was one half of that of *N. pumilio* (Figure 1(a)) and needles did not show any sign of shredder feeding during 4 months indicating that the failure of shredders to consume such tough litter contributed to this difference.

The colonization patterns in the two treatments were similar in terms of total individual numbers, but different in terms of total biomass (Figure 1). These discrepancies were due to the size of individuals that colonized the litter inside the bags (Figure 2a). Large shredders such as the plecopteran *Klapopteryx kuscheli* and the trichopteran *Parasericostoma cristatum* were only found in the *Nothofagus* bags and not in the *Pinus* ones. The dissimilar colonization displayed by large shredders would reflect a preference for *N. pumilio*. Although leaf litter in streams is primarily a food source for shredders (Minshall, 1984), terrestrial debris may also be very important as a refuge and substratum for invertebrates (Reice, 1980). For example, Dobson (1994) found that the number, biomass and diversity of invertebrates colonizing litter bags decreased in high quality litter, because shredder consumption depleted the resource. In the present study

the decay of *N. pumilio* was not high enough to limit the resource and thereby cause a decrease in shredder numbers. On the other hand, *Pinus* needles were also colonized by a high number of macroinvertebrates, especially dominated by gathering-collectors. Since pine needles are tough and have low nitrogen content (Friberg and Jacobsen, 1994; Albariño and Balseiro, 2001), it seems that this low quality leaf pack acted as a natural filter both by trapping fine particulate matter and being a suitable surface for biofilm development. In consequence, throughout the experiment pine needles were more important as a refuge and substratum for both functional feeding groups studied than as a food resource itself.

The second experiment investigated the relationship between invertebrate size and the decay rates of *N. pumilio* leaf litter. The mesh size of open bags allowed large shredders such as *K. kuscheli*, *Monocosmoecus* sp. and *Tipula* sp. to colonize and consume the leaves, while only small macroinvertebrates gained access to the closed bags. The invertebrate assemblage in open bags showed a pattern similar to that observed for *Nothofagus* treatment in the first experiment. Gathering-collectors were constantly dominant in number and represented by small specimens while shredder biomass was dominant as a result of its high individual biomass (Figure 2(b)). Both total shredder density and biomass were low in the closed bags compared with the open ones (Figure 3(d), and 3(e)). Open bags, with a broader size spectrum of shredders, had higher decay rates. Rounick and Winterbourn (1983) and Stewart (1992) found similar results in shredder-rich streams (New Zealand and South Africa, respectively) when they conducted comparable enclosure/exclosure leaf litter breakdown experiments. Also Campbell *et al.* (1994) obtained identical results in an Australian stream. Those studies registered higher differences between treatments than in these experiments because of the very small mesh size used in their 'closed bag' treatment (180–300 $\mu$m). The relatively large mesh size (1000 $\mu$m) used in the closed bags of the present study made them more permeable to small invertebrate colonization and this may have been the reason for the lower differences observed. During the 135 day period, leaf litter in closed bags decayed by 51%. On the assumption that 6% of mass loss at day 7 resulted from leaching and microbial activity, the remaining mass loss (49%) during the experiment should be related both to microbes and small shredders. However, with these treatments, it is not possible to differentiate microbial activity from that of small detritivores. The fact that shredder feeding signs and leaf fragmentation were conspicuous and increased throughout the experiment suggests that small shredders are likely to have some influence in leaf decay. It was assumed that physical leaf fragmentation did not occur because the leaf bags acted as shelter against water and suspended sediment abrasion (Campbell *et al.*, 1994). Short *et al.* (1980) pointed out that small shredders can produce similar results to large ones. Early instars are known to display higher consumption rates per body mass than late ones (Scriber and Slansky, 1981). In a previous experimental study on *N. pumilio* breakdown, Albariño and Balseiro (1998) found that smaller larvae of *K. kuscheli* consumed significantly more leaf litter than large ones, achieving a consumption rate of 0.24% body dry mass day$^{-1}$. However, shredder biomass in open bags was significantly higher than that in closed ones, and this resulted in higher breakdown activity. Although shredder size was directly related with decay rate, the activity of small shredders in Andean headwaters cannot be neglected.

The south mountain beech *Nothofagus pumilio* forms pure stands that characterize the upper belt of Andean-patagonian headwaters (Hildebrand-Vogel *et al.*, 1990). Therefore, the input and breakdown timing of *N. pumilio* leaf litter might be key elements of ecosystem functioning. These experiments showed that the use of exotic Pinaceae with different leaf characteristics resulted in changes to invertebrate colonization and feeding patterns influencing leaf litter decay. Although pine needles may be consumed by aquatic invertebrates (Grafius and Anderson, 1980; Friberg and Jacobsen, 1999), they would only be accessible later than native deciduous leaves. Moreover, the longer leaf litter conditioning time required is likely to lead to a higher probability of downstream transport by seasonal floods. Thus, pine needles would be more prone to export than to *in situ* processing. In consequence, pine detritus entering Andean streams as the main food source may delay or disrupt shredder life cycles. Friberg and Jacobsen (1994) mentioned a similar situation for *Fagus* woodland replacement with pine plantations in Sweden. Furthermore, the

timing of litter input is different between the two tree species. *N. pumilio* is a deciduous tree with an autumn pulse of leaf fall, while pines produce litter all year round with higher amounts in summer (Bray and Gorham, 1964). This difference in litter pulses may also have great effect on shredder populations, although this was not investigated in these experiments.

   The fact that in experiment 1, large shredders were found only in *Nothofagus* bags, and not in pine ones, would indicate that large shredders are not attracted by this litter. Invertebrate movements in searching suitable food patches would consume not only energy and time, which might have been allocated to secondary production, but would also increase predation losses. Both consequences have detrimental effects on large shredder populations. Experiment 2 demonstrated that large shredders are a key to the leaf litter decay of *Nothofagus* leaves. If these large shredders were disadvantaged due to an increment of pine needles in the coarse organic matter standing crop, the whole litter processing mechanism would be affected, with consequences for the entire stream biota. The estimate of suitable areas in Patagonia for pine forestation made by Schlichter and Laclau (1998) suggests that great impacts on aquatic ecosystems can be expected as a consequence of changing litter quality and input timing.

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