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Riparian leaf litter processing by benthic macroinvertebrates in a woodland stream of central Chile

Procesamiento de detritus ripariano por macroinvertebrados bentónicos en un estero boscoso de Chile central

CLAUDIO VALDOVINOS

Unidad de Sistemas Acuáticos, Centro Universitario Internacional Europa-Lationoamérica de Investigación y Formación de Ciencias Ambientales (EULA), Universidad de Concepción, Casilla 160-C, Concepción, Chile, e-mail: cvaldovi@udec.cl

ABSTRACT

Leaf litter input from riparian landscapes has been identified as both a major energy flow to stream ecosystems and as a food source for stream macroinvertebrates. In riparian landscapes of woodland streams of central Chile, the native deciduous hardwoods are being artificially replaced by exotic coniferous trees at a large spatial scale. It is suggested that this process has a significant impact on the stream communities of central Chile. Today, exotic plantations occur throughout central Chile, with *Pinus radiata* (D. Don) (Monterrey pine) accounting for about 80 % of the more than 1,800,000 ha of exotic forests. The objective of this paper was to analyze the effect of the litter beds of a dominant native species (*Nothofagus pumilio*) and an exotic species (*P. radiata*) on the detritus processing carried out by benthic macroinvertebrates, in an experimental catchment of central Chile (Rucúe Creek; 36° 26'00" S, 71° 35'40" W). Results revealed that processing rates of native leaf packs are higher than rates of coniferous leaf packs, suggesting that the replacement of the native hardwoods by exotic coniferous riparian flora has an important impact on the stream energy flow in central Chile. The decay rate coefficients (k) were 0.0072 for *N. pumilio*, and 0.0027 for *P. radiata*. The greater abundance and biomass of shredders per gram of leaf pack of native *Nothofagus* would explain the differences in leaf processing rates, especially through the activity of two Plecoptera Gripopterygidae, *Limnoperla jaffueli* and *Antarctoperla michaelseni*.

Key words: macroinvertebrates, leaf processing, stream ecosystem, Chile, exotic plantations, riparian vegetation.

RESUMEN

La entrada de detritus foliar procedente de áreas riparianas ha sido reconocido como un componente importante en la energética de ecosistemas fluviales y como fuente de alimento de macroinvertebrados acuáticos. En áreas riparianas de esteros boscosos de Chile central los componentes nativos caducifolios están siendo artificialmente reemplazados a gran escala por coníferas exóticas, sugiriendo que este proceso tiene un importante impacto sobre las características energéticas de las comunidades fluviales de Chile central. Actualmente, los bosques exóticos existentes en esta área están compuestos principalmente por *Pinus radiata* (D. Don) (pino insigne), llegando a cerca. del 80 % de las más de 1.800.000 ha de plantaciones forestales. El objetivo de este estudio fue analizar el efecto de camadas de hojas de una especie nativa dominante (*Nothofagus pumilio*) y una especie exótica (*P. radiata*) sobre el procesamiento de detritus realizado por macroinvertebrados bentónicos, en una cuenca experimental de Chile central (estero Rucúe; 36° 20' 00" S, 71° 47'40" O). Los resultados muestran que las tasas de procesamiento de los paquetes de hojas de la especie nativa son superiores a la exótica, sugiriendo que la sustitución de la flora nativa caducifolia por coníferas exóticas tiene un importante impacto sobre los componentes energéticos de los ecosistemas fluviales de Chile central. Los coeficientes de pérdida (k) fueron 0,0072 para *N. pumilio* y 0,0027 para *P. radiata*. La abundancia y biomasa de fragmentadores por gramo de paquete de hojas explican las diferencias en las tasas de procesamiento de hojas, especialmente dos plecópteros Gripopterygidae, *Limnoperla jaffueli* y *Antarctoperla michaelseni.*

Palabras clave: macroinvertebrados, procesamiento de hojas, ecosistema fluvial, Chile, plantaciones exóticas, vegetación riparina.

INTRODUCTION

Riparian environments are both ecotones between terrestrial and aquatic ecosystems as well as habitat corridors across regions. These transitional environments serve diverse functions and have different values depending on their physical, biological, and cultural setting (Malanson 1995). Leaf litter input from riparian landscapes has been identified both as a major energetic component of stream ecosystems and as a food source for stream macroinvertebrates (Flory & Milner 1999). In small, heavily shaded streams, there is normally insufficient light to support substantial instream photosynthesis so energy pathways are largely supported by imported (allochthonous) energy sources (Benfield 1996). The bulk of imported energy enters such streams as autumnal leaf fall although additional leaf material may slide or blow into the stream from riparian zones during the rest of the year (Lamberty & Gregory 1996). Leaves falling into streams may be transported over short distances but usually are caught by structures in the streambed forming leaf litter beds (Flory & Milner 1999). These leaves are processed in place by components of the stream invertebrate and microbial community in a series of well documented steps (e.g., Anderson & Sedell 1979, Jones & Momot 1981, Anderson & Danell 1982, Wissmar 1991, Culbert & France 1995, France 1995, Benfield 1996, Flory & Milner 1999).

Leaf processing by benthic macroinvertebrates is an integrative ecosystem-level process because it links elements as leaf species, microbial activity, and physical and chemical features of the stream (Friberg & Winterbourn 1997). The major result of this linkage is that whole leaves are converted into fine particles, which are then distributed downstream and used as energy source by various consumers. Rates of leaf litter processing have been measured in a variety of stream types in the northern hemisphere (e.g., Petersen & Cummins 1974, Sedell et al. 1975, Benfield et al. 1977, Bärlocher et al. 1978, Short et al. 1980). These and other studies have indicated that macroinvertebrates may play an important role in the processing of leaf material. Furthermore, leaf litter has been shown to be an important factor in the distribution of benthic macroinvertebrates in streams (Flory & Milner 1999).

Although many aspects of the structure and function of forest stream ecosystems have been investigated in recent years (Cushing et al. 1995), the effect of forest type on benthic community structure is still poorly understood (Friberg & Winterbourn 1997). Nevertheless, the replacement of native forest or afforestation of grassland catchments with coniferous tree species is an increasingly common practice in many countries. This is especially so where economic policies are resulting in a reduction of agricultural production (e.g., Kuusela 1994). The question therefore arises: does the catchment-scale establishment of exotic plantation forests alter the biotic communities of streams? Several investigations in the northern hemisphere indicate that conifer plantations can affect benthic communities in a negative way compared with other types of catchment vegetation, such as hardwoods (e.g., Harriman & Morrison 1982, Ormerod et al. 1989).

The present study of leaf litter processing was conducted in central Chile where conifer plantations started early in the 20[th] century. Today, exotic plantations occur throughout central Chile, with *Pinus radiata* (D. Don) (Monterrey pine) accounting for about 80 % of the more than 1,800,000 ha of exotic forests (González et al. 1999). In riparian landscapes of woodland streams of central Chile, the native deciduous tree species (e.g., *Nothofagus pumilio*) are being artificially replaced by large-scale by industrial plantations of *Pinus radiata*, suggesting that this process of change in land cover has an important impact on stream community and energetics in central Chile. The objective of this paper was to compare the processing rate of leaf litter beds of a dominant native tree species (*N. pumilio*) and an exotic tree species (*P. radiata*) by benthic macroinvertebrates in an experimental basin of central Chile (Rucúe Creek). Currently, natural forests dominate this experimental area. However, and based on current trends, forest cover dominated by *N. pumilio* will probably be replaced by *P. radiata* in the next decades, affecting downstream ecosystems.

MATERIAL AND METHODS

Study site

Rucúe Creek is located in central Chile in the Biobío river catchment. It is a third-order stream with a watershed area of 227 km^2 and 32.5 km in length. The study site is located at 36° 26' 00" S, 71° 35' 40" W, at an elevation of about 1,050 m above sea level where the stream emerges from a narrow valley with a dense canopy of lenga (*N. pumilio*), and ciprés de la cordillera (*Austrocedrus chilensis*). *Pinus radiata* is a dominant tree species on industrially managed areas and in the lower part of the basin, without influencing the study site. All of the higher part of the basin is covered by native forest which influences the study site.

The study site corresponded to a transitional altitudinal zone between two types of forest cover; *N. pumilio* was the dominant tree species at the upper part of the site (1,000-1,900 m), whereas *Austrocedrus chilensis* was the dominant species at the lower part (700-1,000 m). Leaves of *N. pumilio* fall into the stream and are transported down to the study site. Some of them are caught by structures of the stream bed forming leaf litter beds. Leaf litter beds in the study site were mainly composed by *N. pumilio* (> 98 % dry-weight), followed by *A. chilensis* and unidentifiable detritus (< 2 % dry-weight). According to Hildebrant-Vogel et al. (1990), *N. pumilio* presents one of the most extensive latitudinal range of distribution along the temperate forest of South America, between 35° 35' and 55° 30' S (ca. 2,300 km north-south distribution). In southern Chile the altitudinal range varies between 0 to 700 m (Cuevas & Arroyo 1999). However, near to the northern extreme of distribution altitude varies between 1,300 and 2,000 m (Donoso 1993), which correspond to the altitudinal range observed in the study area.

Stream width varied from 4 to 10 m with an average slope of 7 %. The substrate consisted mainly of rubble in riffles and a few pools. Stream flow was moderated during the study period (3.50 to 10.0 $m^3 s^{-1}$). Nutrients were present at low concentrations (total-P = 0.01-0.02 mg l^{-1}; total-N, 0.11-0.14 mg l^{-1}). The water was soft (9.2-10.1 mg l^{-1} $CaCO_3$), and the pH was close to neutral (7.0-7.3). Dissolved oxygen was always near 100 % saturation.

Leaf litter processing by stream fauna

Leaf processing rates were studied with leaf packs placed in mesh bags (after Benfield 1996). Leaves of the native *N. pumilio* and needles of the exotic *P. radiata* (exotic) were collected in riparian areas of Rucúe Creek in autumn 1997. Leaves were collected directly from trees just prior to abscission. Needles were collected in eight plastic traps of 0.5 m^2 in diameter. Leaves and needles were air dried to constant weight (after Benfield 1996), weighed into 5 g packs, and placed in mesh bags (3 mm mesh size). Additional packs were filled with similar sized sections of black polythene instead of leaves of *N. pumilio* as controls. Both leaf (and needles) and plastic packs were lashed to a brick and placed in a riffle area of the stream on winter 1997. Four packs of each type were removed from the stream in a downstream to upstream direction after 7, 27, 61, 90, and 146 days. At the time of collection, the brick was removed from the stream; the pack was cut free and placed into a plastic bag. Samples were processed within 4 h after collection to minimize possible weight loss of leaf material.

In the laboratory, each leaf pack was thoroughly rinsed with tap water to remove accumulated sediment and particulate organic matter. Macroinvertebrates were separated from the material and preserved in 80 % ethanol. The intact leaves were dried at 60 °C for 48 h and the weight determined (± 0.1 g). Absolute loss of weight and percentage of the initial weight remaining were determined. Macroinvertebrates removed from the leaf packs were identified, enumerated, and their weight determined after drying to constant weight at 60 °C. No attempt was made to correct for loss of weight due to preservation. Macroinvertebrates were assigned to functional groups according to information in Merritt & Cummins (1996), and by inspection of gut contents (Table 1).

A laboratory study was conducted to determine weight loss of leaf material attributable to leaching. Pre-weighed amounts (0.1 g) of air dried leaves (*N. pumilio*) and needles (*P. radiata*) were placed separately into small jars containing 150 ml of stream water. These jars were placed inside constant-temperature chambers maintained at 6 and 14 °C. Five jars of each leaf type from each temperature were removed at intervals of 24, 48, 72, and 168 h. The remaining leaf material was dried at 60 °C for 48 h, and weighed to determine loses of material.

Following Benfield (1996), fall-winter leaf processing was assumed to follow an exponential decay model of the form $Y_t = Y_0 e^{-kt}$ where Y_t is the amount remaining after time t of the initial amount Y_0 (after leaching), and k is the loss rate or processing coefficient. Following $\log_e$ transformation of the remaining percentage data, linear regression was used to estimate the processing coefficient for each leaf species after excluding leaching loss. According to Benfield (1996), processing coefficients were compared statistically using analysis of covariance (ANCOVA).

RESULTS AND DISCUSSION

Leaf litter processing revealed that native deciduous leaf packs (*N. pumilio*) were processed at a faster rate than exotic coniferous leaf packs (*P. radiata*), suggesting that the replacement of the native trees by exotic riparian flora has an important impact on the energetics of stream community in central Chile. The abundance and biomass of shredders per gram of leaf pack is a

TABLE 1

General classification system for aquatic insect trophic relations. This classification is applicable only to immature and adult stages that occur in the water (modified from Merrit & Cummins 1996)

Sistema general de clasificación de relaciones tróficas de insectos acuáticos. Esta clasificación es aplicable sólo a estados acuáticos inmaduros y adultos (modificada de Merrit & Cummins 1996)

Functional group (based on feeding mechanisms)	Subdivision of functional group: Dominant food	Feeding mechanism	Range of food particle size (µm)
Shredders	Decomposing vascular plant tissue-coarse particulate organic matter (CPOM)	Detritivores-chewers of CPOM	$> 10^3$
	Living vascular hydrophyte plant tissue	Herbivores-chewers and miners of live macrophytes	
	Wood	Gougers-excavate and gallery, wood	
Collectors	Decomposing fine particulate organic matter (FPOM)	Detritivores-filterers or suspension feeders of FPOM	$< 10^3$
		Detritivores-grazing scapers of mineral and organic surfaces	
Scrapers	Periphyton-attached algae and associated material	Hervivores-pierce tissues or cells and suck fluids	10^2 - 10^3
Predators	Living animal tissue	Engulfers-carnivores, attack prey and ingest whole animals or parts	$> 10^3$
		Piecers-carnivores, attack prey, pierce tissues and cells, and suck fluids	

likely explanation for the differences in leaf processing, especially by two Plecoptera Gripopterygidae, *Limnoperla jaffueli* and *Antarctoperla michaelseni*.

The greatest loss of weight due to leaching (168 h laboratory experiments) occurred in *N. pumilio* (20.3 %) and the least in *P. radiata* (3.6 %) (mean values from Table 2). The main loss of weight for each leaf type occurred within the first 24 h after immersion. Results showed no influence of temperature on leaching between 6 and 14 °C for both species (at 24 h: *N. pumilio*, $F_{(1,8)} = 0.30$, $P = 0.60$; *P. radiata* $F_{(1,8)} = 0.21$, $P = 0.66$). In situ weight loss of leaf packs over time is shown in Fig. 1. Percent loss of weight after 7 days in the stream were not significantly different from the 168 h laboratory leaching experiments for each species (at 14 °C: *N. pumilio*, $F_{(1,7)} = 1.56$, $P = 0.70$; *P. radiata*, $F_{(1,7)} = 2.76$, $P = 0.14$), indicating that leaching was mainly responsible for the initial

TABLE 2

Loss of weight (percent loss of initial mass ± SD) of leaf material due to leaching at different temperatures

Pérdida de masa (porcentaje de pérdida de la masa inicial ± SD) del material foliar debido a lixiviación a diferentes temperaturas

Leaching time (h)	*Nothofagus pumilio* 6 °C	*Nothofagus pumilio* 14 °C	*Pinus radiata* 6 °C	*Pinus radiata* 14 °C
24	12.8 ± 6.5	14.3 ± 4.1	3.6 ± 1.1	4.2 ± 1.6
48	20.3 ± 3.9	18.2 ± 6.3	5.2 ± 0.7	3.8 ± 0.8
72	15.1 ± 8.2	11.3 ± 3.7	4.9 ± 0.9	5.0 ± 1.4
168	18.3 ± 4.5	13.1 ± 4.6	5.0 ± 0.8	4.7 ± 0.9

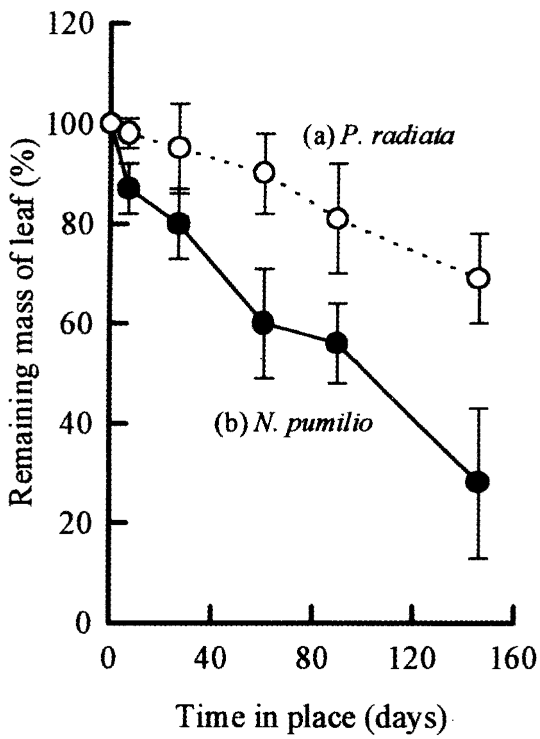

Fig. 1: Loss of mass of leaf litter packs (mean ± SD) in Rucúe Creek, central Chile. (a) Exotic conifer (*Pinus radiata*), (b) native deciduous tree species (*Nothofagus pumilio*).

Pérdida de masa de paquetes de hojas (promedio ± DE) en el estero Rucúe, Chile central. (a) Especie de conífera exótica (*Pinus radiata*), (b) especie decídua nativa (*Nothofagus pumilio*).

loss of mass in Rucúe Creek. Following $\log_e$ transformation of the "remaining percentage" data (Fig. 1), linear regressions were used to estimate the processing coefficient for each leaf species after excluding the leaching loss. Both equations were significant ($P < 0.05$), and the data fit well the exponential model. After leaching, *N. pumilio* showed the most rapid degradation. The loss rate coefficient (k) was 0.0072 and 0.0027 for *N. pumilio* and *P. radiata*, respectively. The difference between these coefficients was statistically significant ($F_{(1,47)} = 74{,}24$, $P < 0.0001$); *N. pumilio* was processed at such a rapid rate that after 146 days in the stream little material remained, except for the more resistant veins and midribs. Although direct comparisons with leaf processing rates measured in other studies are difficult to interpret due to the differences in the leaf pack construction, leaf pack size, and water temperature, leaf processing rates of this study are within the reported values for conifers and deciduous trees in other temperate forest of the northern hemisphere (i.e., Petersen & Cummins 1974, Sedell et al. 1975, Bärlocher et al. 1978, Short et al. 1980; Table 3).

Moderate to high densities of macroinvertebrates on leaf packs and controls were obtained after 7 days in the stream (Fig. 2). Initially, collectors exhibited the highest densities in *N. pumilio, P. radiata* and plastic controls, mainly due to the presence of taxa such as *Orthocladius sp.* and *Simulium* sp. In the case of

TABLE 3

Comparison of leaf litter processing coefficients (k) for species found in this study with data reported for other species in northern hemisphere streams

Comparación de los coeficientes de procesamiento de detritus (k) registrados en este estudio, con datos reportados para otras especies en ríos del hemisferio norte

Species	k	Stream order	Season	Mean temperature (°C)	Reference
Alnus tenuifolia	0.0308	3	Fall-spring	0	Short et al. (1980)
Alnus rubra	0.0168	3	-	4	Sedell et al. (1975)
Salix bebbiana	0.0135	3	Fall-spring	0	Short et al. (1980)
Betula lutea	0.0116	*	-	18	Petersen & Cummins (1974)
Acer saccharum	0.0107	*	-	18	Petersen & Cummins (1974)
Carya grabra	0.0089	*	-	18	Petersen & Cummins (1974)
Salix lucida	0.0078	-	Fall-spring	3-4	Petersen & Cummins (1974)
Populus tremuloides	0.0077	3	Fall-spring	0	Short et al. (1980)
Alnus glutinosa	0.0075	*	-	18	Petersen & Cummins (1974)
Nothofagus pumilio	0.0072	3	Winter-spring	6-14	Present study
Populus tremuloides	0.0046	-	Fall-spring	3-4	Petersen & Cummins (1974)
Quercus alba	0.0038	*	-	18	Petersen & Cummins (1974)
Pinus ponderosa	0.0038	3	Fall-spring	0	Short et al. (1980)
Pinus resinosa	0.0030	-	Fall-spring	-	Bärlocher et al. (1978)
Pinus radiata	0.0027	3	Winter-spring	6-14	Present study
Fagus grandifolia	0.0025	*	-	18	Petersen & Cummins (1974)

*In the laboratory

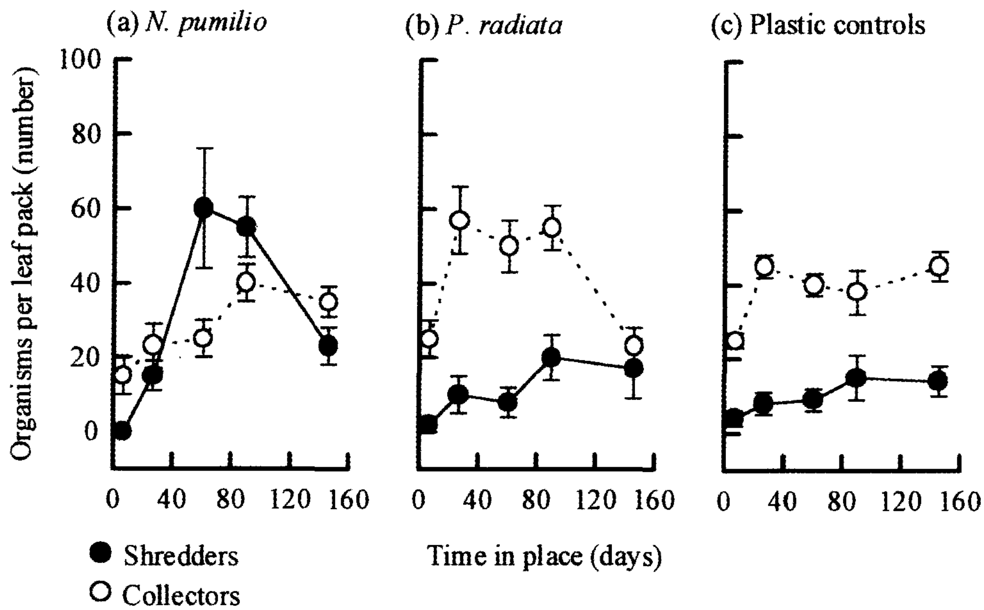

Fig. 2: Colonization of leaf packs in Rucúe Creek, central Chile (mean ± SD), by different functional groups of macroinvertebrates. (a) Native deciduous tree species (*Nothofagus pumilio*), (b) exotic conifer (*Pinus radiata*) and (c) plastic controls.

Colonización de paquetes de hojas en el estero Rucúe, Chile central (promedio ± DE), de acuerdo a la clasificación de grupos funcionales. (a) Especie de conífera exótica (*Pinus radiata*), (b) especie caducifolia nativa (*Nothofagus pumilio*) y (c) hojas de plástico (controles).

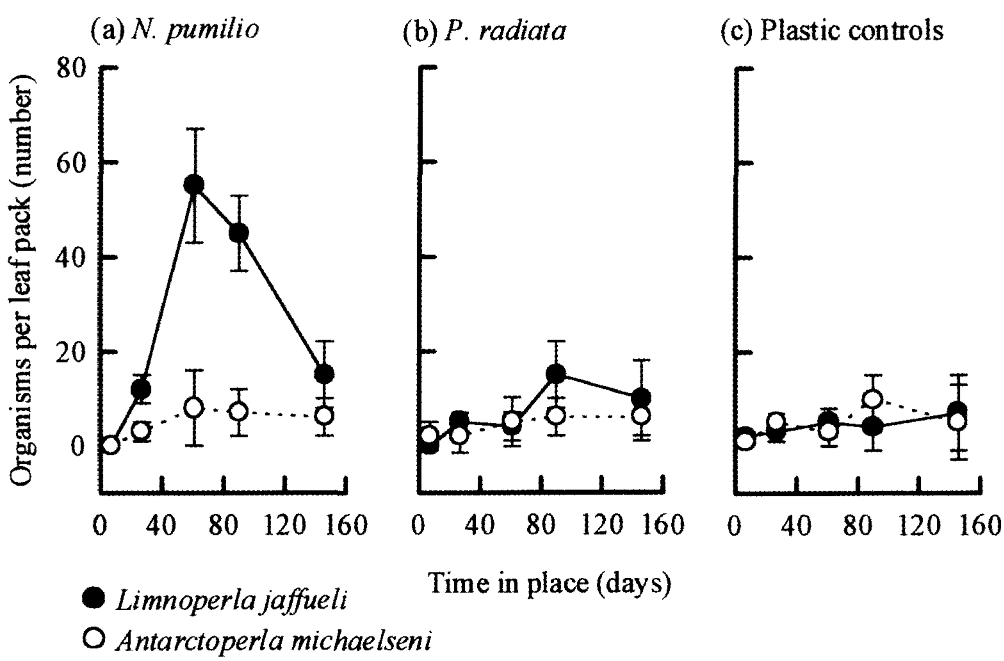

Fig. 3: Temporal occurrence and density (mean ± SD) of two shredder species (*Limnoperla jaffueli* and *Antarctoperla michaelseni*) in *Nothofagus pumilio*, *Pinus radiata* and plastic (controls) "leaf packs" for Rucúe Creek, central Chile.

Ocurrencia temporal y densidad (promedio ± DE) de dos especies de fragmentadores (*Limnoperla jaffueli* y *Antarctoperla michaelseni*) en *Nothofagus pumilio* (lenga), *Pinus radiata* (pino insigne) y hojas de plástico (controles), en el estero Rucúe, Chile central.

TABLE 4

Macroinvertebrate taxa identified from leaf packs in Rucúe Creek (central Chile). Functional group classification based on Merritt & Cummins (1996): S = shredder, C = collector, G = grazer, and P = predator. All insects are immature stages

Taxa de macroinvertebrados recolectados en paquetes de hojas en el estero Rucúe (Chile central). Clasificación de grupos funcionales basada en Merritt & Cummins (1996): S = fragmentador, C= colector, G = pastoreador y P = depredador. Todos los insectos son estados inmaduros

Taxon	Functional group	*Nothofagus pumilio* (lenga)	*Pinus radiata* (Monterrey pine)	Controls (plastic)
Ephemeroptera				
Meridialaris diguillina	C/G	•		•
Baetis sp.	C	•	•	
Plecoptera				
Limnoperla jaffueli	S	•	•	•
Antarctoperla michaelseni	S	•	•	
Coleoptera				
Elmis sp.	C	•	•	•
Trichoptera				
Smicridea chilensis	C	•	•	•
Diptera				
Simulium sp.	C	•		•
Orthocladius spp.	C	•	•	•
Megaloptera				
Protochauliodes sp.	P	•	•	•
Hydracarina	P	•	•	•
Oligochaeta	?	•	•	•
Total number of taxa		11	9	9

N. pumilio, the density of shredders was higher than that of collectors after 28 days, mainly due to *L. jaffueli* (with a maximum at 61 days). On *P. radiata* and plastic controls, the highest shredder density occurred at 90 days. High shredder densities were not obtained after 146 days in leaf packs and plastic controls probably due to the emergence of winter stoneflies (Fig. 3). Maximum collector densities occurred at 90 days for *N. pumilio* and 27 days for *P. radiata* and controls (Fig. 2). Generally, the same macroinvertebrate taxa colonized the two leaf pack types (Table 4). Exceptions occurred when a few individuals of particular taxa were collected from certain pack types. The most abundant taxa collected were *Orthocladius* sp., *Simulium* sp., *Hydracarina* and *Limnoperla jaffueli*. The dominant shredders were *L. jaffueli* and *A. michaelseni* . Densities of two shredder species on the leaf packs are shown in Fig. 2. Densities of shredders (and total macroinvertebrates) found on the *P. radiata* needle packs and on plastic controls were relatively low.

Shredder abundance on *N. pumilio* leaf packs in Rucúe Creek was significantly different from *P. radiata* packs (at 61 days, $F_{(1,6)} = 81.39$, $P < 0.0001$), and from controls (at 61 days, $F_{(1,6)} = 79.14$, $P < 0.0001$), which suggests that *N. pumilio* leaves were used as a food source. No significant differences in shredder abundance were detected between *P. radiata* packs and plastic controls (at 61 days, $F_{(1,6)} = 0.93$, $P = 0.371$). The biomass of shredders on *N. pumilio* and on *P. radiata* showed clear differences, particularly after 48 days (Fig. 4). The maximum value for *N. pumilio* is approximately similar to the highest value observed in *Populus tremuloides* (aspen) and *Salix* spp. (willow) in an Oregon stream by Short et al. (1980). While in Chilean mountain streams, the shredding process may rest on a few large Perlidae (35-40 mm body length); the Plecoptera shredders in this woodland stream are small-sized. Feeding mode of *L. jaffueli* and *A. michaelseni* also may differ from the larger sized shredders. Whereas the large shredders actually bite off chunks of leaf material, smaller shredders may scrape the leaf surface, removing the cuticle, the epidermis, and the mesophyll (Wallace et al. 1970). The effect of scraping is similar to that reported for

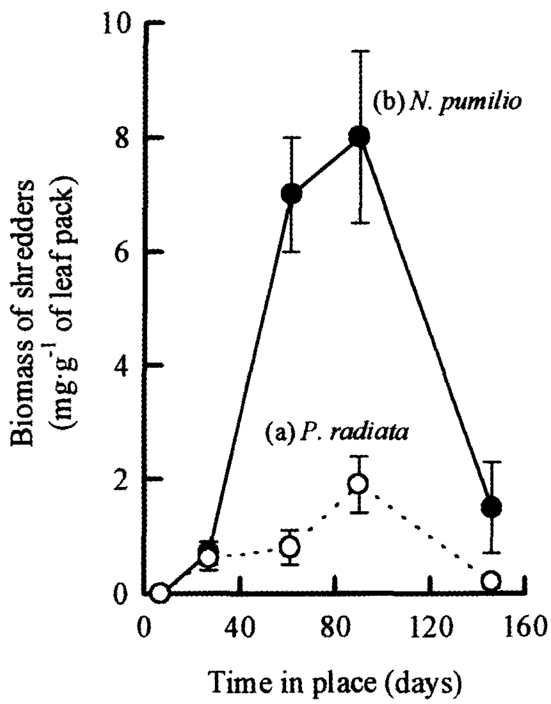

Fig. 4: Biomass of shredders (mg) per gram of leaf pack for Rucúe Creek, central Chile (mean ± SD). (a) Exotic conifer (*Pinus radiata*); (b) native deciduous tree species (*Nothofagus pumilio*).

Biomasa de fragmentadores (mg) por gramo de paquete de hojas, en el estero Rucúe, Chile central (promedio ± DE). (a) Especie de conífera exótica (*Pinus radiata*); (b) especie caducifolia nativa (*Nothofagus pumilio*).

the large shredders *Capnia* and *Nemoura* in the northern hemisphere, which skeletonize leaves and thus decrease leaf weight (Brinck 1949).

Hence, the rate of processing depends on the rate of conditioning (governed by the leaf species) and the intensity of attack by invertebrates. Naturally, this will vary in different streams because of differences in faunal composition (Bird & Kaushik 1981). Shredders also enhance the availability of nutrients to collectors. This has been demonstrated by Short & Maslin (1977), finding that the collectors *Hydropsyche californica* and *Simulium arcticum* accrue significantly greater amounts of ^{32}P in the presence of the shredder, *Pteronarcys californica*. Collectors, which feed on fine particulate organic matter produced by biological shredding activity or mechanical breakdown by abrasion, may increase downstream. Probably, the presence of the predator *Protochauliodes* sp. (Megaloptera) was facilitated indirectly by invertebrate use of leaves because of increased numbers of potential prey species. Also, needles of *P. radiata* and plastic substrates may accumulate periphyton and fine terrestrial matter on their surfaces, which could influence invertebrate colonization (Richardson 1991, Suren & Winterbourn 1992).

Petersen & Cummins (1974) divided leaf processing in streams into leaching, initial microbial processing (or conditioning), and animal-microbial conversion. Physical abrasion may be added to this classification (Bird & Kaushik 1981). The extent to which any of the above sub processes contributes to the overall breakdown will vary with the nature of leaves, water quality, temperature, stream substrate and colonization rates, and benthos activity (Bird & Kaushik 1981). Although many adult insects can disperse to Rucúe Creek from nearby streams, habitat factors probably determine successful colonization. Leaf retention has been suggested as a key factor determining shredder abundance (Rounick & Winterbourn 1982, Townsend & Hildrew 1988, Flory & Milner 1999), and the preferences of certain shredders for different leaf species, is well documented (e.g., Parkyn & Winterbourn 1997). The data presented herein make a similar case for Chilean woodland stream in that high quality leaves such as *N. pumilio* are rapidly processed.

The results about the native deciduous species are obviously valid only for *N. pumilio* and are not directly applicable to other native deciduous or coniferous species. According to the present data and the information published in the literature (e.g., Benfield 1996), the physical and chemical characteristics of the leaf litter beds are more important than the native or exotic conditions, in determining the decay rate coefficients. In this sense, the real impacts in the fluvial landscapes are derived mainly from changes in the quality and quantity of the leaf litter beds. Further investigation on the nutritive value of leaf packs of *N. pumilio* and *P. radiata* is needed to assess more clearly the impact of replacement of native species on the stream trophic structure and fluxes of matter and energy in riparian landscapes in central Chile.

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