

Table of contents

Preface: Ecological advances on Chilean temperate rainforests.....	1
<i>Carlos Oyarzún, Niko E.C. Verhoest, Pascal Boeckx, Roberto Godoy</i>	
Land cover change from primary to secondary lowland forests: effects on tree species composition and C/N ratio of litter and soil.....	5
<i>Cecilia A. Pérez, Martín R. Carmona, Juan C. Aravena, José M. Fariña, Juan J. Armesto</i>	
Frogs and life strategies: an approach to evaluate forest ecosystem health in southern Chile	17
<i>César Cuevas P., Sandra Cifuentes P.</i>	
Temperate ecosystems of Chile: characteristic biogeochemical cycles and disturbance regimes	31
<i>Roberto Godoy, Leandro Paulino, Eduardo Valenzuela, Carlos Oyarzún, Dries Huygens, Pascal Boeckx</i>	
Leaf litter dynamics in headwater streams of the Chilean Andes: influence of shredders and silvicultural activities.....	41
<i>Giovany Guevara, Roberto Godoy, Pascal Boeckx, Carlos Jara, Carlos Oyarzún</i>	
Effects of management practices on water yield in small headwater catchments at Cordillera de los Andes in southern Chile	55
<i>Carlos E. Oyarzún, Jeroen Staelens, Niko E.C. Verhoest, Roberto Godoy</i>	
Changes in abundances of parasitoids (Hymenoptera) and others arthropods (Araneae) in managed and unmanaged native rainforests	65
<i>Yuri Ugarte-Lavados, Paul Dassori A.</i>	
Terrestrial nitrogen cycling in southern Chile: looking back and forward	89
<i>Dries Huygens, Pascal Boeckx</i>	
Aboveground nutrient cycling in temperate forest ecosystems of southern Chile	103
<i>Jeroen Staelens, Carlos Oyarzún, Leonardo Almonacid, Evelyn Padilla, Kris Verheyen</i>	
Ecosystem responses of Andean <i>Araucaria-Nothofagus</i> communities after a wildfire	117
<i>Leandro Paulino, Roberto Godoy, Pascal Boeckx</i>	
Effect of wildfire on soil organic matter in an Andisol of a southern Chilean temperate rain forest.....	133
<i>Yessica Rivas, Roberto Godoy, Dries Huygens, Pascal Boeckx, Francisco Matus, Heike Knicker</i>	
Soil carbon storage in allophanic soils: Study of a temperate pristine rainforest <i>Nothofagus pumilio</i> in the altitudinal limit	147
<i>Francisco Matus, Marcelo Panichini, Roberto Godoy, Fernando Borie</i>	
The old-growth forests in the Valdivian Andes: composition, structure and growth.....	171
<i>Pablo J. Donoso, Leah Samberg, María Paz Hernández, Bastienne Schlegel</i>	
Leaf litter dynamics in a forested small Andean catchment, northern Patagonia, Argentina.....	183
<i>Ricardo Albariño, Verónica Díaz Villanueva, Leonardo Buria</i>	

Preface

Ecological advances on Chilean temperate rainforests

Carlos Oyarzún¹, Niko E.C. Verhoest², Pascal Boeckx³, Roberto Godoy⁴

¹ Instituto de Geociencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: coyarzun@uach.cl

² Laboratory of Hydrology and Water Management, Ghent University, Coupure links 653,
B-9000 Ghent, Belgium. Email: niko.verhoest@ugent.be

³ Laboratory of Applied Physical Chemistry - ISOFYS, Ghent University, Coupure links
653, B-9000 Ghent, Belgium, Email: pascal.boeckx@ugent.be

⁴ Instituto de Botánica, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: rgodoy@uach.cl

This book is the final activity in the framework of 10 years bilateral cooperation between Ghent University (Belgium) and Universidad Austral de Chile (Chile). The bilateral cooperation started on December 1999, when a first bilateral and technological cooperation (BIL 99/4), entitled: “*Comparison of ecosystems functioning and biogeochemical cycles in temperate forests in southern Chile and Flanders*” was funded. In December 2001, a second bilateral scientific and technological cooperation (BIL 01/04) entitled: “*Risk assessment of agricultural intensification on N deposition on pristine forests and plantations in southern Chile*” started. A third bilateral scientific and technological cooperation (BOF2004) entitled: “*Effect of fire damage on regeneration and N loss from Araucaria araucana forest in southern Chile*” was funded in January 2001. The fourth and last bilateral project entitled: “*Ecohydrological Monitoring and Modelling in Managed and Unmanaged Native Forest Ecosystems in Southern Chile*” started in January 2006.

During these cooperations, sixth joint workshops were organized. A first workshop (BIL 99/4) was held in Gent from 17 to 19 September 2001, a second workshop (BIL 99/4) in Valdivia from 11 to 13 November 2002, a third (BIL 01/04) was organized in Gent from 22 to 26 April 2003, a fourth workshop (BIL 01/04) was held in Valdivia from 11 to 13 January 2005, a fifth workshop took place in Gent from 2 to 4 August 2006, and finally a sixth workshop was organized in Valdivia on 16 December 2008. These meetings were accompanied by excursions to relevant Chilean, Belgian and German forests. The results of the first workshop were published in a book: “*Comparison of ecosystem functioning and biogeochemical cycles in temperate forests in southern Chile and Flanders*”, edited by De Schrijver A., Kint V. and Lust N. (eds), Academia Press, Gent, 129 p. The proceedings of the second and the third workshop were published in a special issue

of *Gayana Botanica*, resp. Vol. 60, 2003 and Vol 62, 2005. The papers of the sixth workshop are presented in this book entitled “*Ecological advances on Chilean temperate rainforest*”. These papers cover various aspects of forests management, biogeochemical cycles and soil processes in forested ecosystems and the effects of the forest disturbances on soil, biota and stream ecology.

The first set of contributions deals with the analyses of the composition, structure and growth of the old-growth forests in the Valdivian Andes (Donoso *et al.*) and the effects of the management of these forests on water yield, nitrogen transformations and abundance of parasitoids. Oyarzún *et al.* point out that the reduction of the basal area in both evergreen and deciduous forests leads to a significant increase in water yield. Pérez *et al.* working in a secondary chronosequence and primary lowland evergreen rainforest on Chiloé Island tested the hypothesis that the transformation of primary to secondary forests by fire or selective logging, either industrial or traditional, can alter tree species composition and consequently the quality of organic matter entering the forest floor as well as the heterotrophic microbial processes. Ugarte-Lavados and Dassori reported that the abundance relative of Aculeata (Hymenoptera) increased in ecotones and managed old-growth forests compared to unmanaged old-growth forest, and the same pattern was observed when ecotones and managed secondary forests are compared to unmanaged forests.

Three papers deal with biogeochemical cycling and one paper with soil carbon storage in Chilean allophanic soils. Huygens and Boeckx documented some results of a 10 year lasting journey of bilateral projects in several South Chilean forests. They give results about the ‘pristine, undisturbed’ N cycle, and evaluate disturbance impacts on the microbiological community composition, associated N transformations, and N leaching. Godoy *et al.* summarize historical land use changes and their association with human settlements and analyze how the natural and anthropogenic disturbances in the region modify the dynamics of the natural vegetation and composition of the landscape. Staelens *et al.* quantify nutrient fluxes in varying forest types in southern Chile in order to evaluate external and internal nutrient cycling within ecosystems, with a focus on the aboveground compartment. Matus *et al.* present an overview of the factors and mechanisms involved in the soil carbon storage in Chilean allophanic soils with particular reference to porous steeped (30-70% slopes) volcanic materials occurring in the piedmont and dejections cones of the volcanoes range in south-central Chile.

Two papers present the effects of wildfire on forest communities of *Araucaria-Nothofagus* at the Chilean Andes. Paulino *et al.* assess the effects of fire on the vascular plants regeneration, the N transformations and some enzymatic activities in the soil, as the mycorrhiza colonization parameters on the roots of *Araucaria araucana* seedlings under controlled experimental assay. And Rivas *et al.* analyze the effect of the fire on the quality of soil organic matter (SOM),

quantifies changes in “Black Carbon” content after wildfire, and evaluate the impact of fire on the chemical composition of SOM.

The last three contributions present the effects of forest disturbances on stream ecology and frogs biodiversity. Guevara *et al.* evaluated the leaf litter dynamic processes (input and decomposition) in evergreen (pristine and managed) and deciduous forested streams in the Andes of southern Chile. Albariño *et al.* describe structural and functional aspects associated with detritus dynamics in a *Nothofagus pumilio* forest small watershed located in the driest extreme of the eastwardly pluvial gradient in northern Patagonia. Finally, Cuevas and Cifuentes evaluate frog diversity and life strategies as indicators of forest ecosystems health in southern Chile.

The Flemish part was funded by the Ministry of the Flemish Community, Science, Innovation and Media Department. The Chilean research groups were supported by the Dirección de Investigación y Desarrollo, Universidad Austral de Chile and several Fondecyt projects. We especially thank Prof. Dr. Oswald Van Cleemput for his collaboration in the revision of the manuscripts.

Land cover change from primary to secondary lowland forests: effects on tree species composition and C/N ratio of litter and soil.

Cecilia A. Pérez¹, Martín R. Carmona², Juan C. Aravena³, José M. Fariña¹,
Juan J. Armesto^{1,2}

¹Center for Advanced Studies in Ecology & Biodiversity (CASEB), Departamento de Ecología, Pontificia Universidad Católica de Chile. Alameda 340, Santiago, Chile,
Email: cperez@bio.puc.cl, jmfarina@bio.puc.cl, jarmesto@bio.puc.cl

²Instituto de Ecología y Biodiversidad (IEB), Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile. Las Palmeras 3425, Santiago, Chile,
Email: mcarmonao@gmail.com

³Center for Quaternary Studies (CEQUA), Avenida Bulnes 1890, Punta Arenas, Chile,
Email: Juan.Aravena@cequa.cl

Abstract. The transformation of primary to secondary forests by fire or selective logging, either industrial or traditional, can alter tree species composition and consequently the quality of organic matter entering the forest floor as well as the heterotrophic microbial processes. We tested this hypothesis in a secondary chronosequence and primary lowland evergreen rainforest on Chiloé Island, southern Chile. Principal Component and Correspondence Analysis of tree species composition, basal areas, and soil chemical and physical variables showed a significant segregation of secondary chronosequences dominated by North Patagonian species and primary old-growth forests dominated by species of the Valdivian rainforest. The main ordination axis was significantly associated with differences in soil and litter C/N ratio's, net N mineralization, soil pH, water content and bulk density. We conclude that changes in the floristic composition due to fire and selective logging results in changes in soil litter quality, where the soils of the Valdivian rainforest are better drained, have a higher pH, a lower C/N ratio of litter and surface soil, associated with higher net N mineralization rates, than soils of North Patagonian rainforests. The pools of total carbon (6318-8321 kg C ha⁻¹) and nitrogen (246-444 kg N ha⁻¹) remained similar in all forests. This is linked to the similar litterfall inputs to the forest floor (1111-1491 g m⁻² day⁻¹), except for the early successional sites.

1. Introduction

Lowland temperate forests are commonly affected by human land use because of their location on the most productive soils and their accessibility. The main changes in cover are conversions from primary forest to either agricultural or forest plantations and to pasture land or secondary forests. Industrial logging tends to

convert large areas of originally primary forests into plantations or secondary forest. Extensive land use changes have taken place for about four centuries in South-Central Chile [1,2]. However, only very recently the effects of such changes on ecosystem processes are being assessed [3,4,5,6,7,8,9,10].

On Chiloé Island (42° S), mainly during the second half of the 20th century, primary forests have been transformed into secondary forests by two main types of anthropogenic disturbances; first, by the use of fire to clear land for pastures or agriculture, which may be later abandoned. This land use is often accompanied by traditional selective cutting, whereby small landowners remove fuelwood and timber for construction, transforming primary to secondary forests. This land use leaves behind a fragmented landscape, consisting of a mosaic of secondary forests of different ages, or times since abandonment, surrounded by open pastures and shrublands [11,12,3]. More recently, industrial selective logging of primary forests, requiring a management plan approved by CONAF (Chilean Forest Service), has become a second and widespread form of disturbance to the Chiloé forests. The logging practice consists of extraction of selected timber species for construction of wooden panels, especially large trees from primary forests leaving in place about 35% of the canopy cover. This is followed by removal of canopy trees through selective logging. Open canopy stands are immediately invaded by a dense cover of native bamboo (*Chusquea* spp.), which are normally limited to canopy gaps in undisturbed, old-growth stands [13].

One of the best documented changes in forest ecosystems after anthropogenic disturbance and land cover change can be seen in the pool of total carbon in soils [14,15,16,17,18]. These authors found that the change in land cover from forest to crops reduces the pool of carbon by 30% and that of nitrogen by 15%. Land cover change from native forest to exotic conifer plantation reduces soil carbon by about 10%. However, some land cover changes can also produce an increase in soil carbon content. Examples are the conversion from crops to industrial tree plantations or the recovery of cropland to secondary forest [16]. In contrast, there is much less understanding of the effects of land cover change from primary to secondary forests, following successional recovery of disturbed forests. This change is widespread in areas where forests are being cleared or affected by industrial logging [e.g. 19]. This phenomenon is relevant in southern temperate forests where few remnants of old-growth forests are becoming encroached by expanding secondary forests [2]. The consequences of this land cover change for ecosystem functions are almost completely unknown.

We hypothesize that fire and selective logging change the floristic composition and structure of lowland primary rainforests forests, thus altering litter quality and the pools of carbon and nitrogen in soil. The objective of this paper was to examine this hypothesis by comparing the effects of land cover change from primary to secondary forest on the quality of soil organic matter, soil carbon and nitrogen pools

and soil processes associated to heterotrophic bacteria, such as net nitrogen mineralization and nitrogen fixation.

2. Methods

2.1 Study Sites

In lowland areas of the northern Chiloé Island, we selected eight sites representing a secondary chronosequence of stands recovering from anthropogenic fire, conformed by two early (ES), three mid (MS) and three late successional (LS) stages (Table I).

Table I. Characteristics of the forest stands studied in Chiloé Island

Successional stage (code name)	Dominant tree species	Minimum stand Age (years)	Main type of disturbance
Early (ES1)	<i>Drimys- Amomyrtus</i>	2	Anthropogenic fire- limited SC
Early (ES2)	<i>Nothofagus- Drimys</i>	11	Anthropogenic fire- limited SC
Mid (MS1)	<i>Nothofagus- Drimys- Podocarpus</i>	34	Anthropogenic fire- limited SC
Mid (MS2)	<i>Drimys- Eucryphia</i>	51	Anthropogenic fire- limited SC
Mid (MS3)	<i>Nothofagus- Drimys</i>	62	Anthropogenic fire- limited SC
Late (LS1)	<i>Drimys-Laurelia</i>	133	Old-growth, limited SC
Late (LS2)	<i>Nothofagus- Drimys- Podocarpus</i>	134	Old-growth, limited SC
Late (LS3)	<i>Nothofagus- Tepualia- Saxegothea</i>	129	Old-growth, limited SC
Primary (OG-1)	<i>Eucryphia- Luma- Aextoxicon</i>	300	Old-growth, tree fall gaps only
Primary (OG-2)	<i>Laurelipsis- Myrceugenia</i>	~300	Old-growth, tree fall gaps only
Logged in 1997 (SC)	<i>Laurelia- Myrceugenia</i>	~300	Stand-scale selective logging

ES-MS forests have been created by anthropogenic disturbance due to low intensity fire, often followed by low-impact, traditional selective cutting. Late successional stands have not been burnt or industrially logged, but may have suffered from

limited selective cuttings by local landowners (Table I). In addition, we sampled two primary old-growth forests (OG), subjected only to natural disturbance by tree fall (Table I) and one forest site subjected to stand-scale industrial selective logging (SC) (40-50% of the canopy removed), following an approved management plan in the year 1997. In lowland primary forests, the prevailing disturbance regime is associated with tree fall generated by windstorms [20,21]. All sites are located within 50 and 200 m above sea level in the north and central portions of the Chiloé Island (Fig. 1).

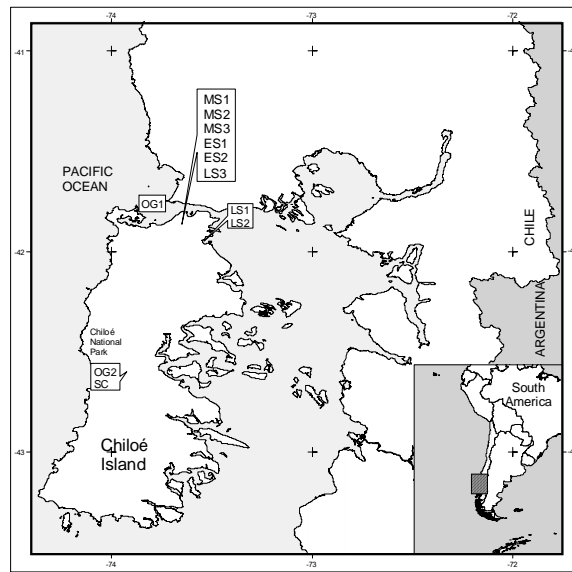


Fig. 1. Map of the study region, showing the location of the study sites

For a more detailed description of the dominant tree species, forest types and soils of the study sites see [3] and [12]. The prevailing climate of lowland Chiloé Island is wet-temperate with a strong oceanic influence [22]. Meteorological records (3 years) at the Senda Darwin Biological Station (41° 53' S, 73° 40' W) indicate an annual rainfall of 2035 mm and a mean annual temperature of 8.7°C. Soil types at all sites are originated from glacial outwash plains, varying in depth from 30 to 80 cm. Soil texture at all sites is silty loam with a high content of organic matter (ca. 33% total carbon).

Permanent plots (50 x 20 m) were set up in each of the 11 forest stands (Table I). In each plot the basal area of all trees larger than 5 cm in trunk diameter at breast height was estimated. In each plot, we set up 6 sampling points and seasonally collected samples of surface soil (A_h horizon) and litter (O_1 horizon) during the years 1999-2001 in the sites representing the chronosequence, and during 2002-2003 in the sites with primary rainforests. The soil variables analyzed were the following: available nitrogen content (N_{disp}), determined in a $KAl(SO_4)_2$ solution; pools of total carbon (C_{pool}) and nitrogen (N_{pool}), determined by flash combustion; *in situ* monthly rates of net nitrogen mineralization (N_{min}), determined by the buried bag method [3], and non-symbiotic N fixation (N_{fix}), estimated by the

acetylene reduction technique [3]. In addition, we characterized the soils by measuring pH-H₂O, bulk density (dens.) and water content (% H₂O), determined gravimetrically. For a more detailed description of the laboratory analyses see [3]. Seasonal values were averaged to obtain annual values.

2.2. Statistical Analyses

In order to assess the differences among sites in a bi-dimensional space, we reduced the number of soil variables and floristic (woody species composition) differences into two principal axis, by applying two multivariate ordination techniques to the data matrices [23]. Sites and forest types were arranged according to the tree species composition and basal areas by a correspondence analysis (CA). This type of analysis was more appropriated than PCA (Principal Component Analysis), considering the high amount of zeros in the raw matrix due to the absence of species. Ordination of study sites according to soil variables was conducted through a PCA. The degree of significance of principal component's axes and the weighed coefficients for the variables were assessed by a Montecarlo randomization test using the statistical packages Pop Tools and MVSP.

3. Results

The sites ordination obtained from a CA of the basal cover of trees clearly separates in one extreme of axis 1 the primary forests and the site with conventional selective cutting and in the other extreme the secondary forests (ES, MS and LS) that underwent fire and non-conventional selective cutting (SC) (Fig. 2).

These sites are grouped regardless of successional stages. Axis 1 explain 33.5% of the variability and axis 2; 19.1%, together they explain 52.6% of the variation in tree species composition and basal area. The species that compose the group of primary old-growth rainforests (OG) are those described as characteristics of the Valdivian rainforest such as *Laureliopsis philippiana*, *Aextoxicon punctatum*, and different *Myrtaceae* species (Fig. 3). The species that compose the group of secondary rainforests are those described as characteristics of the North Patagonian rainforest with *Nothofagus nitida*, *Podocarpus nubigena*, *Drimys winteri*, *Weinmania trichosperma*, *Tepualia stipularis*. However, there are also some species described as characteristics of the Valdivian rain forest such as *Eucryphia cordifolia* and *Gevuina avellana* (Fig. 3).

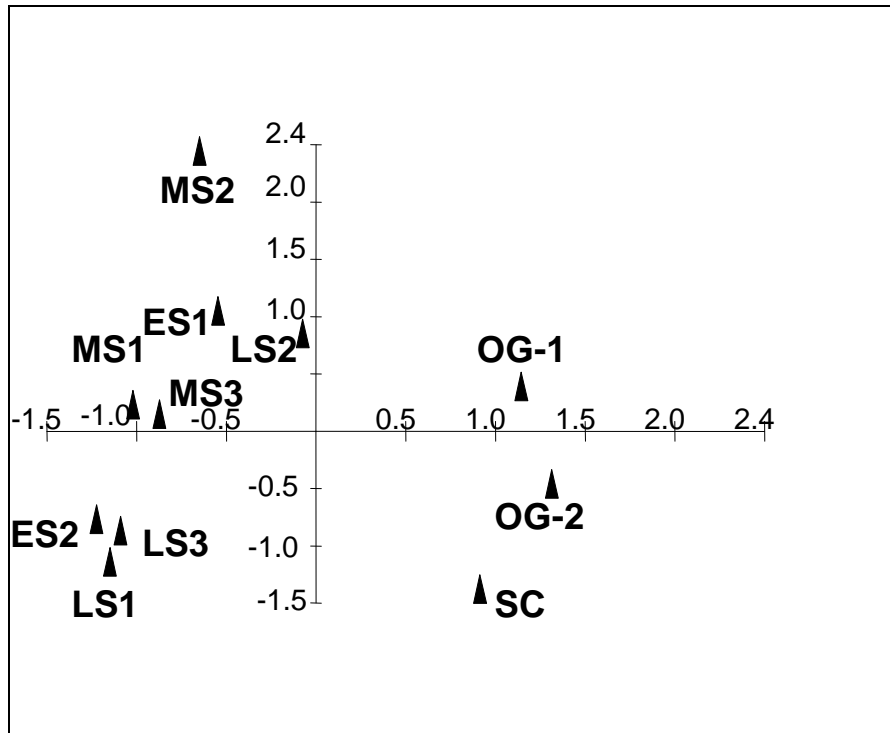


Fig. 2: Site ordination according to a correspondence analysis based on basal cover of trees. Abbreviations of sites are given in Table I.

The PCA ordination of sites according to physical and chemical properties of soils (Fig. 4) is generally coincident with the 2-dimensional ordination of stands based on tree species composition and basal areas. Therefore, it reflects primarily differences among forest types (Table I). At one end, primary forests dominated by *Laureliopsis* and *Aextoxicon* are grouped together with the floristically similar site subjected to industrial selective logging. North Patagonian forest stands recovering from fire and late successional forests are grouped at the opposite end of axis 1. Axis 1 explains 58% of this variation (Fig. 4). The logged Valdivian forest stand appears segregated from its primary forest counterparts along axis 2, although this difference was not significant, according to Monte Carlo randomization test.

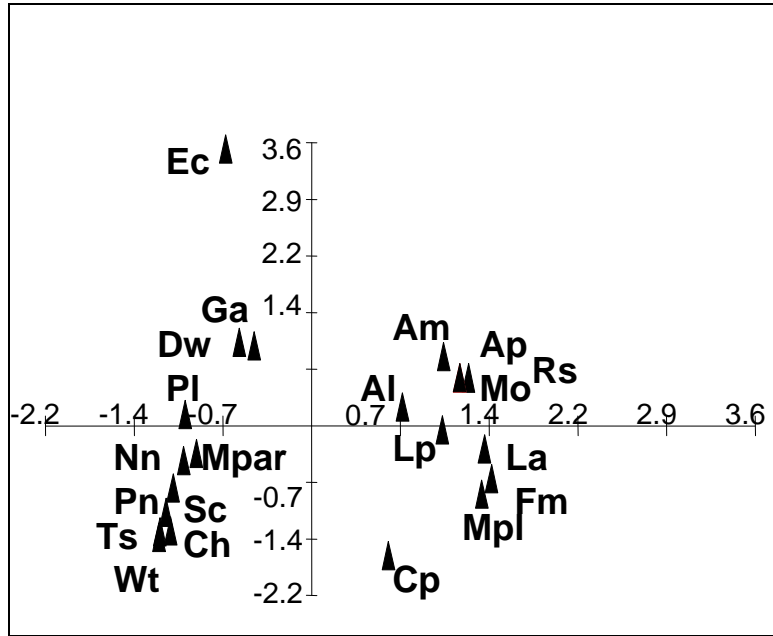


Fig. 3: Tree species ordination for successional and primary forest stands according to a correspondence analysis based on basal cover of trees. *Ap*: *Aextoxicon punctatum*, *Lp*: *Laureliopsis phillipiana*, *Mo*: *Myrceugenia ovata*, *Rs*: *Rhaphithamnus spinosus*, *Am*: *Amomyrtus meli*, *Al*: *Amomyrtus luma*, *La*: *Luma apiculata*, *Fm*: *Fuchsia megellanica*, *Mpl*: *Myrceugenia planipes*, *Cp*: *Caldcluvia paniculata*, *Ec*: *Eucriphya cordifolia*, *Ga*: *Gevuina avellana*, *Nn*: *Nothofagus nitida*, *Pn*: *Podocarpus nubigena*, *Sc*: *Saxegothea conspicua*, *Ts*: *Tepualia stipularis*, *Ch*: *Crinodendron hookerianum*, *Dw*: *Drimys winteri*, *Pl*: *Pseudopanax laetevirens*, *Wt*. *Weinmania trichosperma*, *Mparv*: *Myrceugenia parviflora*

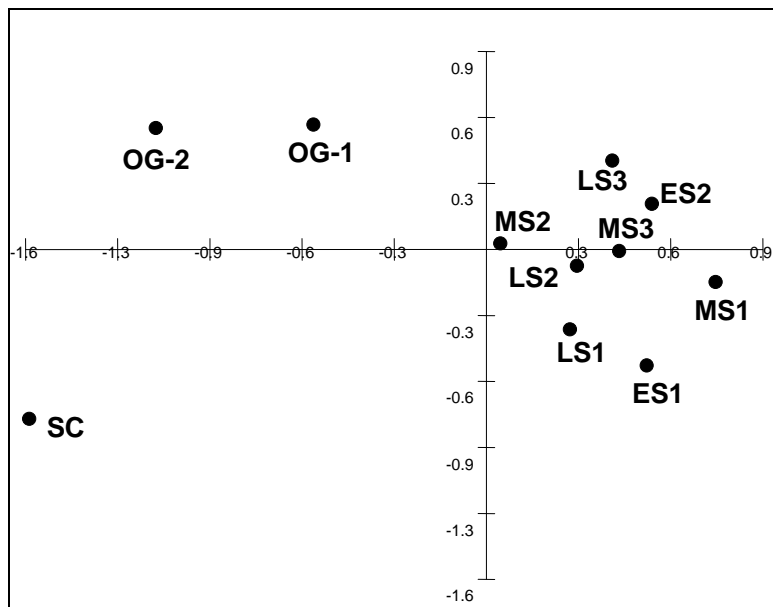


Fig. 4: Site ordination according to a principal Component Analysis based on the chemical and physical variables of surface soils. Site abbreviations as in Table I .

The soil variables that significantly contributed to the pattern of segregation of sites in the 2-dimensional ordination (Fig. 5) are the following: soil and litter C/N ratio's, net N mineralization, water content, pH and bulk density. The positive end of axis 1 has a concentration of North Patagonian old-growth forest sites and secondary forest sites, with higher litter and soil C/N ratio's, lower rates of net N mineralization, more acid pH, lower bulk density, and a higher soil water content. At the opposite end of axis 1, we find the two Valdivian primary forests dominated by *Aextoxicon* and *Laureliopsis*, together with the selectively logged neighboring site.

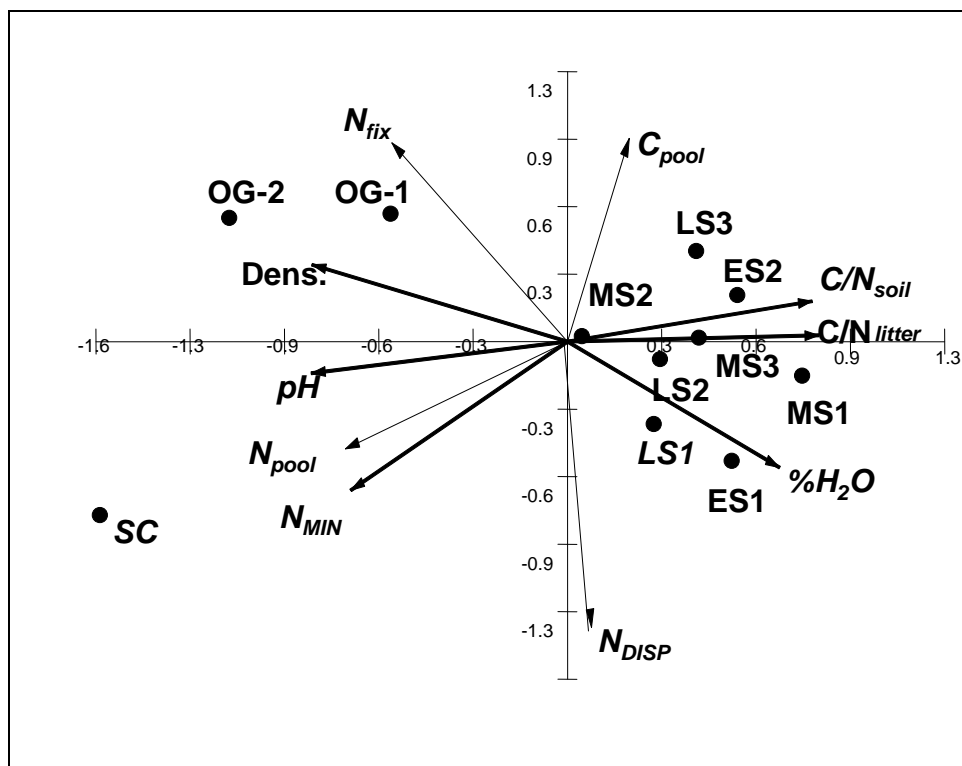


Fig. 5. Soil variables that significantly contribute to site ordination in a Principal Component Analysis as indicated by thicker vectors. Site abbreviations as in Table I, soil variables abbreviation in Methods

The average values obtained per stand age show that Valdivian and North Patagonian rainforests do not differ in carbon and nitrogen pools, but they do differ in the quality of soil organic matter. The Valdivian forest sites had lower litter and soil C/N ratio's. Litterfall was only significantly lower in the ES sites (Tab.II).

Table II. Average carbon and nitrogen pools, C/N ratio of surface soil and litter layer and litter flux in a secondary chronosequence and primary old-growth lowland rainforest in Chiloé Island

	Cpool (kg ha ⁻¹)	Npool (kg ha ⁻¹)	C/N A _h	C/N O ₁	Litter flux [†] (g m ⁻² d ⁻¹)
Early successional (N=2)	7438±2641	246±56	29.8± 4.0	58.9±2.9	0.138±0.083
Mid successional (N=3)	7626±828	292±47	26.5±4.4	60.4±4.0	1.253±0.398
Late successional (N=3)	8321±1408	313±21	26.8±5.4	51.7±9.0	1.111±0.555
Old-growth primary (N=2)	7802±1496	441±95.1	17.7±0.4	33.6±8.3	1.279±0.107
Selective cutting (N=1)	6318±1398	444±110	14.3±0.65	29.3±2.3	1.259±0.363

[†] Samples from 6 randomly located litter traps taken from March 2003 to April 2005 in the secondary chronosequence and from February 2004-April 2005 in old-growth primary and selective cuttings.

4. Discussion

The temperate forest on the Chiloé Island can be described as a mosaic composed mainly by these two forest types: the Valdivian rainforest, generally associated with milder, more oceanic temperature conditions, occurring on deeper and better drained soils, and distributed up to 250 m elevation; and the North Patagonian rainforest, associated with cooler summer temperatures, less rich and shallower sites, often with poor drainage, and occupying the altitudinal range from 250 to 600 m height of the Coastal Range of the Chiloé Island and South-Central Chile [24,25,26]. Besides this spatial variation in both forest types, temporal variation also occurred. Palinological evidence shows that climate change during the Holocene on the Chiloé Island, promotes the expansion of Valdivian rain forests during dry-hot episodes and the expansion of North Patagonian forests during wet-colder episodes [27]. This and the results presented here suggest that this climatic changes in the past brought together changes in soil drainage and biogeochemical processes in soil, promoting changes in the floristic composition of forests.

Here we postulate that current fires and selective logging of lowland primary rain forests, either industrial or traditional, can contribute to differentiation among both forest types, leading to the dominance of species that are characteristic of the North

Patagonian rainforest. In such a case, the characteristic species of the Valdivian rainforest such as *Eucryphia cordifolia*, *Aextoxicon punctatum* and *Laureliopsis philippiana* are being selectively logged and replaced by North Patagonian species such as *Nothofagus nitida*, *Drimys winteri* and *Podocarpus nubigena*. Changes in the floristic composition lead to changes in the quality of organic matter entering the forest floor in the following way. In North Patagonian rain forests, a higher C/N ratio of litter produces a higher C/N ratio of soils, with lower bulk density, a higher water content, more acid pH and a lower rate of net N mineralization as compared to Valdivian rain forests. The forest under industrial selective logging is grouped together with primary rainforests because the dominant and shade intolerant understory species *Chusquea quila* has a low C/N ratio of leaf and litterfall (Pérez et al. unpublished data).

The lack of difference in total carbon and nitrogen content that we report here is associated with a lack of difference in fine litterfall input to the forests floor (except in the early successional forests), but from this, we cannot anticipate the effects of repeated or chronic disturbances on the forest carbon and nitrogen pools, which has already changed the quality of soil organic matter, a key driver of decomposition rates.

Acknowledgements

Funding for this work was provided by grants from Fondecyt 1990946, Fondecyt 1050830, Fondap-Fondecyt 1501-0001 to the Center for Advanced Studies in Ecology & Biodiversity and to IEB P05-002 ICM.

References

- [1] J.J. Armesto, C. Donoso, and C. Villagrán “Desde la era glacial a la industrial: La historia del bosque templado chileno” *Ambiente y Desarrollo* (Chile), 10, 64-71, 1994.
- [2] C. Donoso, and A. Lara, Utilización de los bosques nativos en Chile: pasado, presente y futuro. In: Armesto JJ, Villagrán C, Arroyo MT (eds) *Ecología de los Bosques Nativos de Chile*, Editorial Universitaria, Santiago, Chile, pp 71-99, 1996.
- [3] C.A. Pérez, M. R. Carmona, J. C. Aravena, and J. J. Armesto “Successional changes in soil nitrogen availability, non symbiotic nitrogen fixation and carbon/nitrogen ratio in southern Chilean forests ecosystems” *Oecologia*, 140, 617-625, 2004.
- [4] R. Godoy, J. Haneke, J. Staelens, C. Oyarzún, L. Paulino, and M. Barrientos “Dry deposition of nitrogen to passive samplers in grassland and forests canopies in the central depression of southern Chile”, *Gayana Bot.*, 62(2), 110-119, 2005.

- [5] C. Oyarzún, R. Godoy, J. Staelens, C. Aracena, and J. Proschle “Nitrogen fluxes in a *Nothofagus obliqua* forest and a *Pinus radiata* plantation in the central valley of southern Chile” *Gayana Bot.*, 62(2), 88-97, 2005.
- [6] J. Staelens, R. Godoy, C. Oyarzún, K. Thibo, and K. Verheyen “Nitrogen fluxes in throughfall and litterfall in two *Nothofagus* forests in southern Chile”, *Gayana Bot.*, 62(2), 63-71, 2005.
- [7] J. G. Cuevas, D. Soto, I. Arismendi, M. Pino, A. Lara, and C. Oyarzún “Relating land cover to stream properties in southern Chilean watersheds: trade- off between geographic scale, sample size, and explicative power” *Biogeochemistry*, 81, 313-329, 2006.
- [8] Y. Rivas, R. Godoy, E. Valenzuela, J. Leiva, C. Oyarzún, and M. Alvear, “Actividad biológica del suelo en dos bosques de *Nothofagus* del centro-sur de Chile”, *Gayana Bot.*, 64(1), 81-92, 2007.
- [9] C. Oyarzún, C. Aracena, P. Rutherford, R. Godoy, and A. Deschrijver “Effects of land use conversion from native forests to exotic plantations on nitrogen and phosphorus retention in catchments of southern Chile”, *Water Air Soil Pollution* 179, 341-350, 2007.
- [10] S. E. Pérez, C.A. Pérez, M.R. Carmona, J.M Fariña, and J.J Armesto “Efectos del fósforo y carbono lábiles en la fijación no simbiótica del N₂ en hojarasca de bosques siempreverdes manejados y no manejados de la Isla de Chiloé, Chile”, *Revista Chilena de Historia Natural*, 81, 267-278, 2008.
- [11] M.F. Wilson, and J.J. Armesto “The natural history of Chiloé: on Darwin’s trail” *Revista Chilena de Historia Natural*, 69, 149-161, 1996.
- [12] J.C Aravena, M.R. Carmona, C.A. Pérez, and J.J. Armesto “Changes in tree species richness, stand structure, and soil properties in a successional chronosequence in northern Chiloé Island, Chile” *Revista Chilena de Historia Natural*, 75, 339-360, 2002.
- [13] T.T. Veblen, and P.B. Alaback, A comparative review of forest dynamics and disturbance in the temperate rainforests of North and South America. In Lawford, R.G., P.B. Alaback, and E. Fuentes (eds) *High Latitude Rain Forests and Associated Ecosystems of the West Coast of the Americas: Climate, Hydrology, Ecology and Conservation*, vol 116, 173-213, Springer-Verlag, New York, 1996.
- [14] D.W. Johnson, and P.S. Curtis “Effects of forest management on soil C and N storage: meta analysis” *Forest Ecology and Management* 140, 227-238, 2001.
- [15] D. Murty, M.V. Kirschbaum, R.E. McMurtrie, and H. McGilbray “Does conversion of forests to agricultural land change soil carbon and nitrogen? A review of the literature” *Global Change Biology* 8, 105-123, 2002.
- [16] L.B Gou, and R.M. Gifford “Soil carbon stocks and land use change: a meta analysis” *Global Change Biology* 8, 343-360, 2002.
- [17] K.I. Paul, P.J. Polglase, J.G. Nyakuengama, and P.K. Khanna “Change in soil carbon following afforestation” *Forest Ecology and Management* 168, 241-25, 2002.
- [18] R.D. Yanai, W.S. Currie, and C.L. Goodale “Soil carbon dynamics after forest harvest: An ecosystem paradigm reconsidered” *Ecosystems* 6, 197-212, 2003.
- [19] M.E. Harmon, W.K. Ferrel, and J.F. Franklin “Effects on carbon storage of conversion of old-growth forests to young forests” *Science*, 217, 699-702, 1990.

- [20] T.T. Veblen “Forest development in tree-fall gaps in the temperate rain forests of Chile” *National Geographic Research* 1, 161-184, 1985.
- [21] A. Gutierrez, J.J. Armesto, and J.C. Aravena “Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile” *Journal of Ecology* 92, 598-608, 2004.
- [22] F. Di Castri, and E.R. Hajek, *Bioclimatología de Chile*, Vicerrectoría de Comunicaciones, Universidad Católica de Chile, Santiago, 1976
- [23] G.P. Quinn, and M.J. Keough, *Experimental design and data analysis for Biologists*, Cambridge University Press, New York, 2002.
- [24] C. Villagrán “Análisis palinológico de los cambios vegetacionales durante el tardiglacial y postglacial en Chiloé, Chile” *Revista Chilena de Historia Natural*, 58, 57-69, 1985.
- [25] E. Oberdorfer, *Pflanzensoziologische Studien in Chile*. J. Cramer, Weinheim. 1960.
- [26] C. Villagrán “Vegetationsgeschichtliche und pflanzensoziologische Untersuchungen im Vicente Pérez Rosales National Park (Chile) ” *Dissertationes Botanicae*, 54,1-165, 1980.
- [27] A.M. Abarzúa, C. Villagrán, and P. Moreno “Deglacial and postglacial climate history in east-central Isla Grande de Chiloé, southern Chile (43°S)” *Quaternary Research*, 62, 49-59, 2004.

Frogs and life strategies: an approach to evaluate forest ecosystem health in southern Chile

César Cuevas P¹, Sandra Cifuentes P²

¹Instituto de Zoología, Universidad Austral de Chile, Casilla 567 Valdivia, Chile,
E-mail: ccuevas@uach.cl

²Instituto de Ecología y Evolución, Universidad Austral de Chile, Casilla 567 Valdivia,
Chile, E-mail: scifuentes@uach.cl

Abstract. Fragmentation of wooded ecosystems in several parts of the world has reduced the extension and representation of natural habitats for amphibians. These disturbances have been carried out without protecting the size and distribution of the necessary remaining fragments, protecting and preserving the biodiversity or stability of ecosystems. Particularly in the terrestrial systems of the south of Chile, native forests of *Nothofagus* play a key roll in generating a favourable microclimate for anurans species. Preliminary studies indicate a gradual delivery of water into creeks and rivers from basins located in these forests, showing in summer water flows, which are 3-6 times bigger than those of hydrographic basins are with a different soil use (i.e. monocultures). One of the principal causes identified for the decline of the amphibian population is related to the degradation of its habitats, generating propitious conditions for other disorders. Chile possesses a meagre number of amphibian species, reaching not more than 57. The major diversity of anurans (67%) occurs in the Temperate Forest of *Nothofagus* (37°-48° LS). Many of them are endemic and have developed particular adaptation to the environment. Examples are fossorials (nidiculous) reproductive habits (*Eupsophus*), others with a free life tadpole of a mountain stream habitat (*Alsodes* and *Telmatobufo*), or adapted to the edge of a forest and marshes (*Batrachyla*, *Hylorina*), and to the litter of the forest, as well as, to environments of peat bogs (*Phagnum*) where refuges and a high moisture exist (*Rhinoderma*). In this paper, non-disturbed (native forest) and disturbed places (monocultures of exotic plantations) were surveyed, with the main target of determining which frog species occurs in each one and which of them (depending of their life development strategy) can subsist in a disturbed ecosystem. Thus, the anuran communities and their life development strategies were statistically compare with a MDS and a contingency table, respectively. Our results are discussed at the light of previous information concerning the problem of the amphibian declining.

1. Introduction

Fragmentation of woody ecosystems in several parts of the world has reduced the extension and depiction of natural habitats for amphibians [1]. Disturbances have been carried out without attention to the size and distribution of the necessary

remaining fragments, necessary for protection and preservation of biodiversity and ecosystems stability [2]. Particularly, southern Chile *Nothofagus* native forests play a key roll in the generation of the favourable environmental heterogeneity and microclimate for a reduced group of species of anurans [3]. Thus, previous studies indicate that basins provided with native forests, gradually deliver water into creeks and rivers, maintaining in summer water flows which are 3-6 times higher than those of hydrographic basins with a different soil use (i.e. monocultures) [4]. These characteristics are very important to the life of amphibians, especially in dryer seasons.

Chilean frogs have developed a particular and specialised reproductive adaptation to the environmental heterogeneity of the *Nothofagus* ecosystems (Fig. 1) [5]. There are species with a life cycle comprising a benthic free tadpole phase, such as those of *Alsodes* and *Insuetophrynus*. Others are helped by a mouth sucker-like occurring stocked to rocks in the middle of a flow such as *Telmatobufo*. In addition, with free tadpole, species of *Batrachyla* and *Hylorina* occur in more quiet waters in the shore of streams and in marshes inside rush meadows, respectively. Others like *Rhinoderma* have a direct and indirect development and evolve to a neomely strategy (unique in the world) living adapted to the litter of the forest, as well as, peat bog environments (*Phagnum*) where they find refuges and a high moisture level. Finally, some are adapted to the stream border. Species with terrestrial fossorials behaviour (nidicolous, *Eupsophus*) subsist [6].

The main causes suggested for the amphibian declining population at global and local scale are to habitat degradation related [7]. Historically the *Nothofagus* forest suffered degradation by soil use changes e.g., native forest substitution by exotic species of commercial interest (i.e. invaders species), which was accentuated in the last four decades. The particular attributes of life history of amphibians (i.e. cutaneous respiration, aquatic life, dependency on moisture and low temperatures), label them as excellent bio-indicators of the conditions of the environmental health [8]. Although the number of amphibian species is considered to be poor (57 spp., [9]), the highest diversity (67 %) and endemism (77%) of anurans occurs in the Temperate Forest of *Nothofagus* (37° - 48° LS) [10,3]. So, now and in the past, these wooded ecosystems represent the most important habitat for the Chilean amphibian fauna.

In this research, places with a matrix of native forests (i.e. non human-disturbed locations) and those with a matrix of exotic species (*Pinus* or *Eucalyptus*; i.e. human disturbed areas) were surveyed. Therefore, we tried to determine which species were present in each prospected locality, and we investigated the relation between type of habitat (disturbed or not disturbed) and anuran species strategy to adjust to each place, hypothesising that in those disturbed places the amphibian community will be mainly limited to terrestrial and very short free tadpole cycle species. In order to characterize and identify the frog species community, in each

place biodiversity indexes were determined. Our results together with bibliographic information on the prospected localities are discussed.

2. Material and Methods

2.1. Study area

Observations were conducted in eight locations between 34° and 42° LS. Four locations were considered as disturbed locations (with anthropogenic intervention: *Pinus* and *Eucalyptus* plantations) and four were non-disturbed locations (matrix of *Nothofagus* forest = National Park, National reserves or Private Parks) (Fig. 2, and Fig. 3A, B respectively).

2.1.1. Disturbed locations

The disturbed locations were located in Trehualem (35°45'S; 72°37'W, Región del Maule), Ramadillas (37°18'S; 73°17'W Región del Bio-Bio), Chiguayante (36°51'S; 72°59'W Región del Bio-Bio), and Lastarrias (39°15'S; 72°37'W Región de la Araucanía).

2.1.2. Non-disturbed locations

The non-disturbed locations were located in Los Queules Reserve (35°59'S; 72°41'W, Región del Maule), San Pablo de Tregua (39°30'S; 72°02'W, Región de los Ríos), Parque Oncol (39°41'S; 73°18'W Región de los Ríos), and Parque Alerce Andino (41°21'S; 72°21'W, Región de los Lagos).

2.2. Methods

2.2.1. Bibliographic Review

To obtain the number and name of species previously reported in each of the survey sites, a bibliographic review in textbooks and on the internet was conducted.

2.2.2. Sampling Methods

In each location frogs were searched for during 1 hr in different habitats: ecotone, prairie (open areas), and forest. At each site, surveys in randomly selected 20 x 20 m quadrants to estimate the diversity species index were carrying out. Two investigators searched for adults and juveniles using dip nets during 60 min. At each site, three replicated samplings were carrying out. Nine quadrants per site were completed. For each quadrant, a report card, including the number of specimens/species (tadpoles, froglets, adults, male, female, etc.) was completed. In highly heterogeneous areas collections were not time-constrained, rather, each researcher covered a transect trying to do a similar collecting effort.

2.2.3. Diversity index

The following information was collected: E_d = efficiency of detection: $N/N_p \times 100$; DM_g = Specific diversity: $(S-1)/\ln N$; and D_s = species density: Spp/A [11].

2.2.4. Statistical analysis

Multivariate analyses: in order to evaluate similarities among collected anurans' samples, a non-metric multidimensional scaling (MDS) to the batrachofauna composition of the eight localities it was developed. The non-metric MDS along with an analysis SIMPER ("Similarity percentages-species contribution") were complemented to evaluate the dissimilarity percentage of fauna between different sampled localities, based on the similarity matrix calculated with the coefficient of Bray-Curtis. Data were previously transformed with double square root [12].

Contingency tables: Chapter 23 of [12] was followed to construct 2 x 6 contingency tables comparing proportions of six development strategies between the two different environments (disturbed and not disturbed) along the *Nothofagus* forest distribution. The null hypothesis for contingency table testing is that the frequencies of frog's development strategy are independent of the disturbed or not disturbed environments. We used the 5% significance level as indicator of a statistically significant association.

3. Results

3.1. Bibliographic Review

Although already a lot of papers has been published on Chilean batrachofauna from 1810 till today, there is still more detailed taxonomic information on wider zoogeographic areas or National Parks such as the Nahuelbuta Range, the Maulino rainforest or Valdivian rain forest than on the local sites. By the way, in this paper the bibliographic review for anuran species only include information about wider geographical areas (Table I).

3.2. Sampling Methods

A summary of results obtained from the fieldtrip survey is shown in Table II. Those locations where some species were not found or not documented are signed with zero (0) and — (line), respectively. In San Pablo de Tregua, eight of nine species potentially collectable were detected. The nuptial calls of two of them were recognized: *R. darwinii* and *Hylorina sylvatica*, the second one was not collected, but was present.

3.3. Diversity index

The summary of diversity index obtained from the data collection is presented in Table III. The efficiency of detection, the specific diversity, and the number and health of the species in San Pablo de Tregua (non disturbed location) were higher than in the other sites (e.g. Chiguayante and Ramadillas, disturbed location) (Table II). Photograph of frogs from Trehualem and San Pablo de Tregua are showed in Fig. 5.

3.4. Statistical analysis

Multivariate analyses (Fig. 4): the value of stress indicates that this figure is a very good graphic representation of the relations between locations based on the batracofauna composition. The localities Chiguayante (Ch), Lastarrias (Las) and Trehualem (Tre) (grey circles) have more similarities among themselves (more nearby) than when they are compared to the rest of the locations, which were displayed separated from the preceding group and among themselves (white circles). The plot (Fig. 4) suggests that faunal communities (abundance and composition of frogs) registered in human disturbed locations (grey circles; with anthropogenic intervention) are different to those detected in non-disturbed locations (white circles; native forest). An exception was Ramadillas, which appears separated from the rest of the disturbed locations (grey circles). This suggests that the faunal composition was more similar than in the non-disturbed locations, in spite of being an anthropogenic intervention location.

The percentage of dissimilarity between the disturbed locations [grey circles; Chiguayante (Ch), Lastarrias (Las), Trehualem (Tre) and Ramadillas (Ram)] and the non-disturbed locations [white circles; Los Queules (LQ), San Pablo de Tregua (SPT), Alerce Andino Park (PAA) and Oncol Park (PO)] were around 55% and mainly *Als*, *Pt*, *Ba* and *Rhino* species contributing to this differentiation (SIMPER analyses results). The disturbed locations (i.e. grey circles) presented a similarity of 74% among themselves, contributed by species *Pt* and *Eup*, whereas the similarity percentage of the non-disturbed locations was around 64%, given mainly by *Als*, *Eup* and *Ba*.

Contingency table: The result of contingency table (table IV) shows that the development strategy of frog species registered in this study was dependent of the kind of location sampled, suggesting that the subsistence of some anuran species in places with anthropogenic intervention on forests could be related to its development strategy. At present, those locations showing disturbed conditions [Trehualem, Ramadillas, Lastarrias, Chiguayante] conserved species of frogs with a kind of development strategy favourable to environmental conditions with a scant water offer (*Eupsophus* and *Pleurodema*, with terrestrial development and a short free life cycle, respectively) (Fig. 4). In contrast, sampled human non-disturbed locations (Los Queules, Parque Oncol, Alerce Andino, and San Pablo de Tregua)

supported species showing all kind of strategies reported to the *Nothofagus* forest [5] and this work (Table I, Fig. 1).

4. Helpful Hints

4.1. Figures and Tables

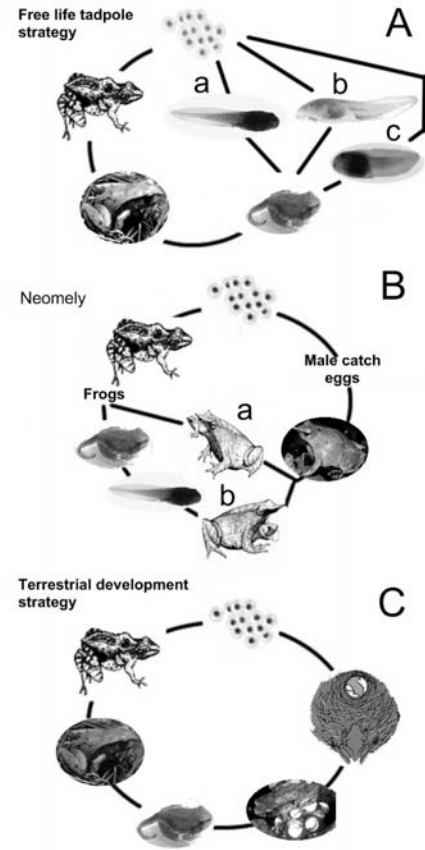
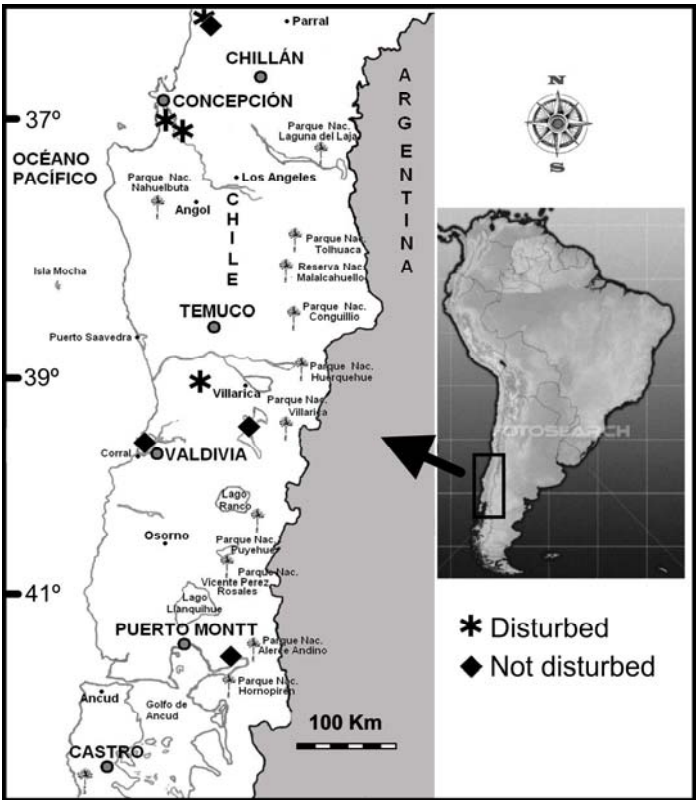


Fig. 1. Scheme of the development strategy of frogs of the *Nothofagus* forest in Central and South Chile. A free life tadpole (a): benthic mountain stream, *Alsodes*, *Insuetophrynus*; (b): mountain stream with mouth sucker-like, *Telmatobufo*, (c): lentic free tadpole (*Batrachyla*, *Hylorina*, *Pleurodema*). B Neomely (a): direct development, *Rhinoderma darwinii*; (b): indirect development, *R. rufum*. C terrestrial development, nidiculous, *Eupsophus*.

Fig. 2. Map showing the 8 locations sampled along Central-South Chile. Scale = 100 km.



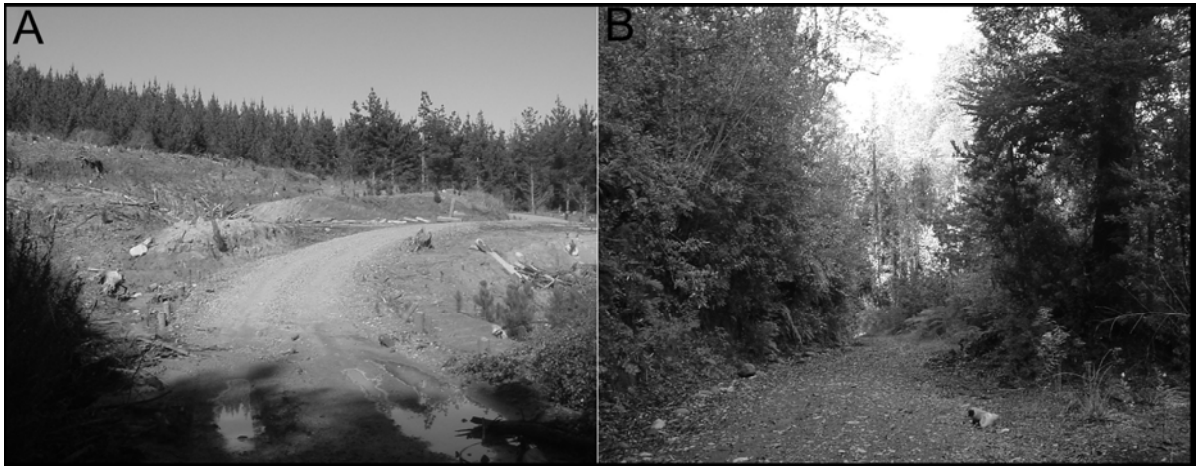


Fig. 3. Examples of A disturbed location (Trehualem), B non-disturbed location (San Pablo de Tregua)

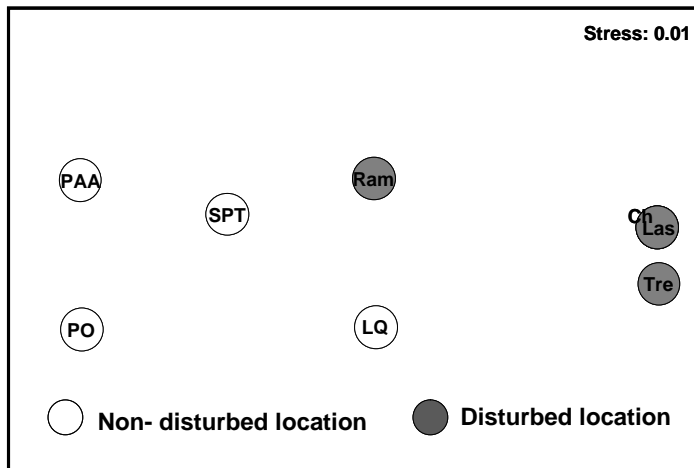


Fig. 4. Non-metric MDS plot based on the abundance of the batracofauna registered in Trehualem (Tre), Chiguayante (Ch), Ramadillas (Ram), Lastarrias (Las), San Pablo de Tregua (SPT), Parque Oncol (PO), Los Queules (LQ) and Parque Alerce Andino (PAA). Analysis based on index of similarity of Bray–Curtis

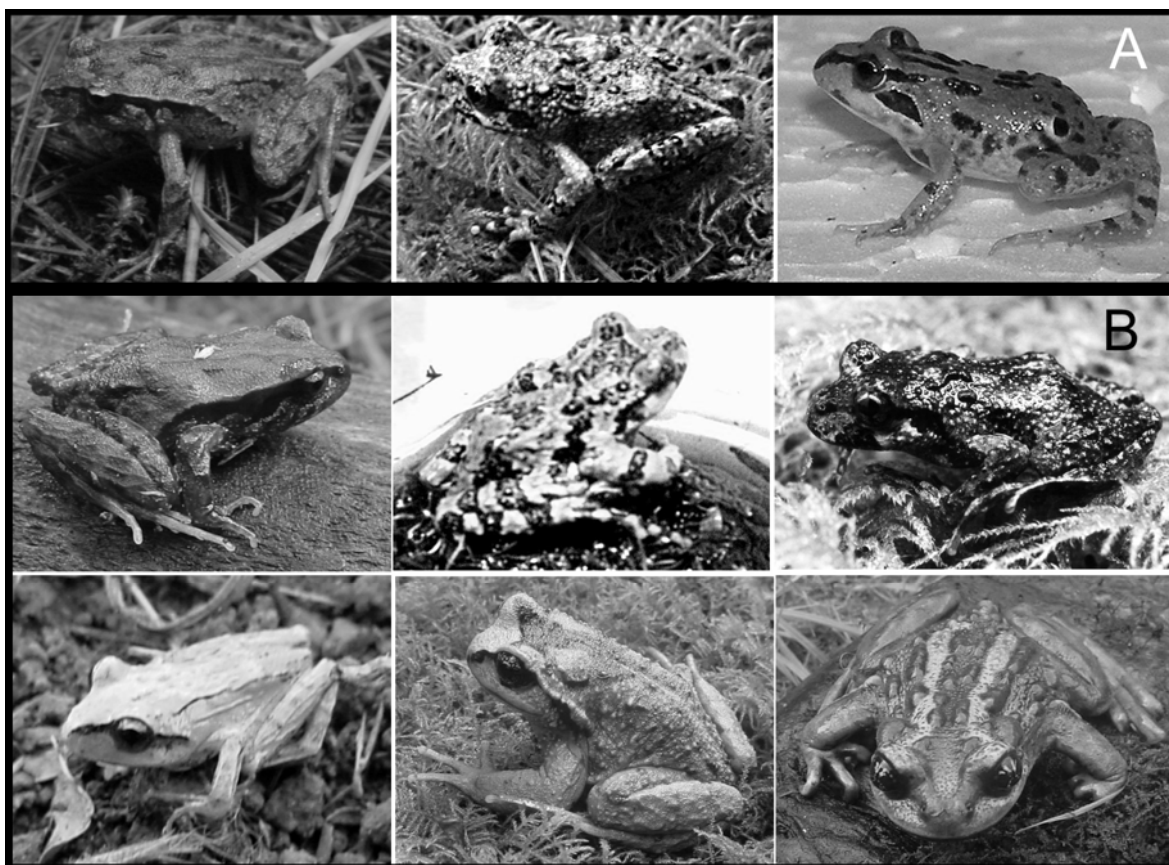


Fig. 5: A Frogs from Trehualem. Left to right, first file: *Eupsophus queulensis*, *Batrachyla leptopus* (first time detected), *Pleurodema thaul*. B Frogs from San Pablo de Tregua. Left to right, second file: *Eupsophus* sp., *Batrachyla antartandica* (first time detected), *B. leptopus*; Third file: *B. taeniata*, *Alsodes* sp. (first time detected), and *Telmatobufo australis*.

Table I. Geographic area, survey locations, taxa and original papers where they were reported.

Geographic area	Survey locations	Anuran taxa documented	References
Maulino Forest	Trehualemu	<i>Bufo</i> , <i>Caudiverbera</i>	Philippi 1902, Cei 1962
	Los Queules	<i>Alsodes</i> , <i>Bufo</i>	
Nahuelbuta Range	Ramadillas	<i>Alsodes</i> (1 sp), <i>Rhinoderma</i> (1 sp), <i>Eupsophus</i> (1 sp), <i>Batrachyla</i> (2 spp), <i>Bufo</i> (1 sp).	Cei 1962, Formas et al. 1975; Formas 1979, Diaz & Veloso 1979.
	Chiguayante	<i>Rhinoderma</i> (2 spp.), <i>Eupsophus</i> (1 sp),	
Valdivian rainforest	Lastarrias	<i>Alsodes</i> (1 sp), <i>Batrachyla</i> (2 spp), <i>Eupsophus</i> (1 sp), <i>Pleurodema</i> (1 sp).	Formas 1979, Cei 1962
	San Pablo de Tregua	<i>Alsodes</i> (1 sp), <i>Batrachyla</i> (3 spp.), <i>Eupsophus</i> (1 sp), <i>Hylorina</i> (1 sp), <i>Pleurodema</i> (1 sp), <i>Rhinoderma</i> (1 sp), <i>Telmatobufo</i> (1 sp)	
	Parque Oncol	<i>Alsodes</i> (1 sp), <i>Batrachyla</i> (2 sp), <i>Rhinoderma</i> (1 sp), <i>Eupsophus</i> (2 spp).	Formas 1979
	Parque Alerce Andino	<i>Alsodes</i> (1 sp), <i>Batrachyla</i> (3 spp), <i>Bufo</i> (1 sp), <i>Eupsophus</i> (2 spp), <i>Rhinoderma</i> (1 sp), <i>Pleurodema</i> (1 sp).	

Table II. Locations and number of anurans collected.

Human disturbed locations	<i>Bufo</i>	<i>Als</i>	<i>Bl</i>	<i>Bt</i>	<i>Telm</i>	<i>Eup</i>	<i>Pt</i>	<i>Rhino</i>
Trehualemu	—	0	0	—	0	7	10	—
Chiguayante	—	—	0	0	—	27	12	0
Ramadillas	0	25	3	2	0	5	20	0
Lastarrias	—	0	0	0	—	6	2	—
Non human disturbed locations	<i>Bufo</i>	<i>Als</i>	<i>Ba</i>	<i>Bl</i>	<i>Bt</i>	<i>Telm</i>	<i>Eup</i>	<i>Rhino</i>
Los Queules	—	25	—	1	—	30	12	10
San Pablo de Tregua	—	50	12	10	9	4	25	15
Parque Oncol	—	10	6	0	0	—	15	0
Parque Alerce Andino	—	5	5	10	6	—	8	0

Abbreviations: *Bufo*: *Bufo rubropunctatus*, *Als*: *Alsodes*, *Bl*: *Batrachyla leptopus*, *Bt*: *B. taeniata*, *Ba*: *B. antartandica*, *Telm*: *Telmatobufo*, *Eup*: *Eupsophus* *Pt*: *Pleurodema thaul*, *Rhino*: *Rhinoderma*. 0= not founded; — = Not documented.

Table III. Summary of the biodiversity index obtained in each location considered in this study.

<i>Surveys locations</i>	<i>Ed</i>	<i>DMg</i>	<i>Ds</i>
	<i>N/Npx100</i>	<i>(S-1)/lnN</i>	<i>Spp/A</i>
Trehualemu	75%	0.27	3
Chiguayante	75%	0.27	2
Ramadillas	80%	1.05	5
Lastarrias	25%	0.27	2
Los Queules	75%	1.05	4
San Pablo Tregua	100%	1.79	9
Parque Oncol	100%	1.60	4
Parque Alerce Andino	75%	1.55	6

Abbreviations: Ed= efficiency of detection, DMg= Specific diversity, Ds= Species density

Table IV. Contingency table showing observed and waited frequencies according the development strategy of anurans in disturbed and non disturbed locations in Central and South Chile

Collect site	Development strategy					
	FBT Of/Ef	FTS Of/Ef	FLT Of/Ef	DD Of/Ef	ID Of/Ef	TD Of/Ef
Disturbed	25/32,8	0/9,7	49/42,2	0/4,01	0/0	45/30,1
Non-disturbed	90/82,9	34/24,3	98/104,8	14/10	0/0	60/74,9
χ^2 with df = 5	33,57					
$\chi^2_{0,05, 5}$	11,07					

Abbreviations: FBT= Free Benthic Tadpole, FTS= Free Tadpole with Suck, FLT= Free Lothic Tadpole, DD= Direct Development, ID= Indirect Development, TD= Terrestrial Development, Of/Ef= Observed frequency/expected frequency

5. Discussion and Conclusion

When we compare our results from disturbed (i.e. exotic species monocultures) and non-disturbed locations (i.e. native forest) with bibliographic data (Table I) of the composition of the amphibian community, differences came mainly from disturbed locations. First, the diversity index showed a more healthy value in the native forest, reinforcing the hypothesis of the degraded environment as main factor affecting the biodiversity of anurans, as indicated by [2]. In this context, land use change is projected to have the largest global impact on biodiversity by the year 2100, as claimed in [13]. In the meantime, these changes are indicative of the occurrence of many ecological processes leading to drastic alterations. We will formulate some preliminary conclusions based on the case of the Chilean anurans and the degradation of their habitat.

Cuevas et al. [3] present preliminary results on the viability of frogs in native forests *versus* exotic plantations (*Pinus* and *Eucalyptus*), which agree with the fact that the original distribution of four of six anurans in critical danger of extinction [*Alsodes vanzolinii* CR A2ac; B2ab (iii), *Eupsophus insularis* CR B1ab (iii), *Insuetophrynus acarpicus* B1ab(iii)+2ab(iii), and *Rhinoderma rufum* CR A2ace] [14] has been documented in geographical regions where the *Nothofagus* forest is more distressed today. Thus, although the local disappearance of some species of anurans probably has a multi causal explanation [7], the particular habitat requirements of amphibians makes it more vulnerable to lost refuges (landscape homogenization), accumulation of stream sediments (by erosion) reducing water flow, and increase of the temperature inside the forest and into the water [1]. On the other hand, as not all species have the same habitat requirements, in those disturbed habitats, characterized by a limited amount of water, more anuran species are successful to survive with strategies against free tadpole (*Eupsophus*) and a very short larval period requiring higher temperatures to reach quickly the end of metamorphosis (*Pleurodema*). Diaz-Páez and Ortiz [15] explained in detail the characteristics of the reproductive behaviour of *P. thaul* making it an opportunistic species and a successful second invader of disturbed environments. This works out in a wider distribution of this species among Chilean anurans, from desert and steppe to woody ecosystems and from sea level to 2500 m high in the Andes Range.

On the other hand, despite *Rhinoderma* (direct development) posses a strategy that might be more successful in adverse conditions (scarce water supply), they also has been affected by loss of refuges, high temperatures (35°C) and solar radiation (because of diurnal and summer habits of this species). The more dramatic case is that of *R. rufum*, which in addition needs enough water availability to complete its metamorphosis (indirect development with free tadpole) [16]. This species was distributed between 33° and 37° LS where the water was always less abundant, and at present this vital resource has been drastically lost in many places in central Chile. This species has not been collected in any place of his original area from 1981 up to now, and could become the first Chilean anuran extinct.

The case of Ramadillas location deserves special attention here. Although this place is one of the more disturbed in the Nahuelbuta Range, it hosted five species and had apparently a healthy biodiversity index, and was different (MDS analysis, Fig. IV) from the rest of the disturbed localities (grey circles), suggesting that the faunal composition was more similar to the non-disturbed locations. From our analyses, it can be seen that this location was outstanding because all species detected occurs in an area of no more than 50 m². Sharing this small and precarious habitat species of *Alsodes*, *Batrachyla*, and *Pleurodema*, which are rarely found together in the wild and in pristine ambient. In fact, *Pleurodema* and *Batrachyla* are secondary invaders of woody disturbed environments and probably *Pleurodema* will be the only one species that in the near future will prevail over the others. This is a clear consequence of habitat homogenization (monocultures), forcing species generally in sympatry, but occupying different ecological niches, to become syntopic. Furthermore, *R. rufum* and *Alsodes vanzolinii* - both species catalogued as “in critical danger of extinction” – both were previously reported in this location.

In [17] as well as in [13] comprehensive research illustrates the importance of biodiversity richness to the functionality of the ecosystem and vice versa. In this sense, our results are better explained through an approach to the current species diversity from development strategy and its success in different environments conditions. Thus, in native forests species with all six strategies were encountered (Fig. 1). This indicates that in those ecosystems humidity, water, refuges and adequate temperature provide adequate conditions for life of frogs. On the other hand, in disturbed locations, mainly *Eupsophus* (terrestrial development) and *Pleurodema* (free life tadpole in warming waters) survive. Therefore, results of this research suggest that the anuran development strategy play a key roll in the determination of which species will prevail in a disturbed ecosystem. Thus, the presence of *P. thaul* in places, where a native forest was the dominant habitat before it became a monoculture with exotic plantations; indicate the strong alterations of the natural conditions.

Our results support the conclusions obtained in previous research demonstrating the negative effect of disturbed forest conditions on the anuran viability [18, 19], as is also the case for other groups of animals [13, 20, 21, 22]. This encourages us to continue sampling more locations to our ongoing study in order to obtain a more representative approach and to allow reaching conclusions that are more rigorous. Chilean Batrachofauna species mostly posses a free tadpole phase, therefore, they need abundant water or moisture to live. In such a scenario, they are facing big troubles!

Acknowledgement

Grant FONDECYT 1050313 for Dr. Roberto Godoy and Co-investigators Dr. Carlos Oyarzún and Dr. Pablo Donoso partially funded the present study. Additional funds were obtained from the Escuela de Graduados Facultad de

Ciencias, Dirección de Postgrado and Dirección de Investigación, Universidad Austral de Chile. Scholarship Conicyt 2004 – 2008.

References

- [1] S. Cushman, “Implications of habitat loss and fragmentation for the conservation of pond breeding amphibians: A review and prospectus” *Biological Conservation*, 128, 231-240, 2006.
- [2] G. Mace, J.L. Gittleman, and A. Purvis, “Preserving the Tree of life” *Science* 5626, 1707-1709, 2003.
- [3] C.C. Cuevas, Y.E. Ugarte, and S.L. Cifuentes, “Diversidad de anfibios anuros en dos sitios localizados dentro de los límites del Bosque Templado” *Actas Segunda Jornadas Econothofagus de la Patagonia*, 2008.
- [4] C.E. Oyarzún, R. Godoy, and A. Sepulveda, “Water and nutrient fluxes in a cool temperate rainforest at the Cordillera de la Costa in southern Chile” *Hydrological Processes*, 12, 1067-1077, 1998.
- [5] J.R. Formas, “Adaptaciones larvarias de los anuros del bosque templado austral de Sudamérica” *Medio Ambiente*, 5, 15-21, 1981.
- [6] C. Úbeda, and J. Núñez, “New parental care behaviours in two telmatobiine genera from temperate Patagonian forests: *Batrachyla* and *Eupsophus* (Anura: Leptodactylidae)” *Amphibia-Reptilia*, 27, 441-444, 2006.
- [7] Global Amphibians Assessment, IUCN, Conservation International, and NatureServe. Global Amphibian Assessment, <www.globalamphibians.org>, 2006.
- [8] C.G. Becker, R. Fonseca, C.F.P. Haddad, R.F. Batista, and P.I. Prado, “Habitat Split and the Global Decline of Amphibians” *Science* 318 1775-1777, 2007.
- [9] D.R. Frost, Electronic Database accessible at [http:// research. amnh. org/ herpetology/amphibia/index.php](http://research.amnh.org/herpetology/amphibia/index.php). American Museum of Natural History, New York, USA., 2007.
- [10] J.R. Formas, Los anfibios anuros del bosque temperado austral de Sudamérica. Monography Museum Natural History University of Kansas, in *The South American Herpetofauna: Its origin, evolution, and dispersal*. Duellman, E.W. ed. Pp. 341-369, 1979.
- [11] M.A. Heyer, R.W. Donnelly, L.A. McDiarmid, C. Hajek, and M.S. Foster, *Measuring and monitoring biological diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. Pp. 1-364. 1994.
- [12] J.H. Zar, *Biostatistical Analysis* (4th Edition), Prentice Hall, New Jersey, Pp. 1-699, 1999.
- [13] F.S. Chapin, E.S. Zavaleta, V.T. Eviner, R.L. Naylor, P.M. Vitousek, H.L. Reynolds, D.U. Hooper, S. Lavorel, O.E. Sala, S.E. Hobbie, M.C. Mack, and S. Díaz, “Consequences of changing biodiversity” *Nature*, 405, 234-242, 2000.
- [14] IUCN, Red List of threatened species. Online reference <http://www.iucnredlist.org/>, 2008.
- [15] H. Díaz-Páez, and J.C. Ortiz, “The reproductive cycle of *Pleurodema thaul* (Anura, Leptodactylidae) in Central Chile” *Amphibia-Reptilia* 22, 431-446, 2001.

- [16] J.R. Formas, E. Pugín, and B. “Jorquera, La identidad del batracio Chileno *Heminctes rufus* Philippi 1902” *Physis* 34, 147-157, 1975.
- [17] O.L. Petchey, Species diversity, species extinction, and ecosystem function, *The American Naturalist*, 2000.
- [18] B.W. Grant, K.L. Brown, G.W. Ferguson, and J.W. Gibbons, Changes in amphibian biodiversity associated with 25 years of pine forest regeneration: implications for biodiversity management, in *Biological Diversity: Problems and challenges* S.K., Majumdar, F.J., Brenner, J.E. Lovich, J.F. Schalles, and E.W. Miller (Eds). The Pennsylvania Academy of Science, New York, Pp. 355-367. 1994.
- [19] R.O. Bustamante, and J.A. Simonetti, “Is *Pinus radiata* invading the native vegetation in Central Chile? Demographic responses in a fragmented forest” *Biological Invasions*, 7, 243-249, 2005.
- [20] R.N. Mack, D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz, “Biotic invasions: Causes, epidemiology, global consequences and control” *Ecological Applications*, 10:689-710, 2000.
- [21] D.U. Hooper, F.S. Chapin, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H. Lawton, D.M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A.J. Symstad, J. Vandermeer, and D.A. Wardle, “Effects of biodiversity on ecosystem functioning a consensus of current knowledge” *Ecology Monograph*, 75, 3-35, 2005.
- [22] J.A. Pounds, and M.L. Crump, “Amphibian declines and climate disturbance: The case of the golden toad and the harlequin frog” *Conservation Biology*, 8, 72-85, 1994.

Temperate ecosystems of Chile: characteristic biogeochemical cycles and disturbance regimes

Roberto Godoy¹, Leandro Paulino², Eduardo Valenzuela³,
Carlos Oyarzún⁴, Dries Huygens⁵, Pascal Boeckx⁶

¹Instituto de Botánica, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: rgodoy@uach.cl

²Departamento de Suelos y Recursos Naturales, Universidad de Concepción, Chillán,
Chile, Email: lpaulino@udec.cl

³Instituto de Microbiología, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: evalenzu@uach.cl

⁴ Instituto de Geociencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: coyarzun@uach.cl

⁵ Ingeniería Agraria y Suelos, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: dries.huygens@ugent.be

⁶ Laboratory of Applied Physical Chemistry - ISOFYS, Ghent University, Belgium ,
Email: pascal.boeckx@ugent.be

Abstract. Old-growth Chilean forests represent an important reserve of pristine, temperate forest ecosystems in the world. However, despite their ecological importance, they are threatened by several natural and anthropogenic disturbances. Precipitation chemistry in southern Chile is one of the cleanest in the world. The forest ecosystems, located in the mountain areas are not yet affected by elevated N deposition. Hydrological N losses from these unpolluted forests occur principally via dissolved organic nitrogen (DON) and the internal N cycle appears to be extremely efficient in conserving and recycling N. However, historic human activities are documented to be an important source of disturbance for natural ecosystems. Historical disturbances in temperate forests of Chile (e.g. via wildfires) are dated from 44,000 years B.P. This indicates an influence of those patterns prior to human settlement, dated at 12,500 years B.P. Since then, several historical events emphasize the narrow relationship between humans and forest ecosystems. Paleobotanical records indicate wild- and human-set fires during the last 3,000 years, being an important source of disturbance in the Chilean forests. Since about 450 years B.P., the European colonization has resulted in significant land use changes, increasing the frequency and intensity of disturbances in the forest ecosystems in Chile, mainly during the last two centuries. Currently, forest logging is the most destructive process in Chilean forests. Anthropogenic activities, such as agriculture, transport and industry, are increasing. These activities may substantially alter the atmospheric N load on forest ecosystems, especially as dry and wet inorganic N deposition. The expansion and intensification of agricultural and livestock activities in the region, considering the incorporation of technological and economic support, will result in a significant increase in milk and beef production. Local farmers use mineral fertilisers and urine-manure slurries to increase pasture and crop yields, which have a major impact on water quality e.g. via leached

nitrates during the winter periods. On the other hand, increasing atmospheric N deposition as a result of ammonia volatilization is to be expected. Despite the documented changes in disturbances and anthropogenic activities, there is a consistent lack of knowledge on the internal C and N cycling, and more specifically its response to ecosystem disturbances and land use change. This is a prerequisite in order to evaluate the influence of historical and prospective disturbances, potentially altering its biogeochemical behavior.

1. Chilean temperate forest ecosystems

The native temperate forests of southern Chile represent a globally significant reserve of the biosphere and more than half of the total surface of temperate forest in the Southern Hemisphere [1]. Lichens, fungi, plants, mammals and bird species constitute a particular biota, especially in relation to their geological, physical and climatic settings, which resulted from their positioning in a biogeographic island [2]. Some taxa are derived from ancient elements in southern Gondwana. The special patterns of habitat use, their ecological role as feeding habits and their function related to pollination and seed dispersal, are important factors with evolutionary relevance [3]. The historical geographic isolation of the region resulted in the highest level of endemic species in the world and, in some cases, a taxonomic singularity (phylogenetic unicity), which are relevant aspects to be considered in the quality of biological diversity [4].

The highest species richness in non-vascular and vascular plant species in Chile is found between 40-42°S [5,6] and 90% of the plant genus are endemic and monotypic [2], suggesting the isolated pattern of these forests and an area of great geological antiquity [5]. Some relict tree species of conifers have the longest recorded lifespan, reaching an age of up to 3,600 years, constituting an excellent historical document for studies in reconstructions of climatic variability [7].

2. Biogeochemical cycles in pristine forests of Chile

Temperate forest ecosystems are nutrient-limited, especially with respect to N [8]. Low parent material availability, low atmospheric deposition inputs, strong dependence on the symbiotic and non-symbiotic N₂ fixation, and high amounts of precipitation, contribute to N limitation in Chilean temperate forest ecosystems [9, 10]. For a better understanding of the complex N cycling patterns at ecosystem level, studies in pristine ecosystems are required to simulate a pre-industrial condition. Chilean temperate forest ecosystems still maintain their pre-industrial patterns of conservative nutrient cycling [10,11,12]. In those environments, N cycling is highly efficient. Different strategies can be identified: litter fall dynamics [13,14], nutrient conservation via long leaf lifespan and conservative physiological processes [15,16,17], specific mycorrhizal symbiosis [18], and non-symbiotic N₂ fixation [19]. The role of some key biogeochemical processes such as heterotrophic nitrification, dissimilatory nitrate reduction to ammonium, and a dissolved inorganic

N (DIN) cycle that operates independently of dissolved organic N (DON) losses are also discussed as mechanisms of N retention in temperate rainforests on volcanic soils in Chile [20].

3. Historic ecosystem disturbance

Biological remains from archeological deposits are an important source of information about human activities and living conditions in the human settlement and past environmental conditions. Monte Verde is a late pleistocene settlement in Southern Chile (41°S) [21]. In the archeological site, plant material was found from different types starting from about 13,000 year B.P. [22]. The presence of several taxa from different vegetation types at distant places from the site, suggests a high human activity and selective exploitation and transport of materials by the early inhabitants [23]. Assuming that these remains were collected for food consumption, this is an indicator of early strong interaction of humans with temperate forest ecosystems. The presence of burned and unburned material remains suggests a controlled and selective use of fire [22].

Charred wood and seeds are the most common plant remains found from archaic deposits dated 8,000 year B.P. This is an important evidence for human activities and living conditions in the temperate forests and their relationship to the aquatic ecosystems in the Araucarian Lakes region [24].

Late-Holocene vegetation record of the Andean Araucaria region obtained from fossil pollen and charcoal showed a repetition of fires and volcanic events that has influenced the regional vegetation [25]. The past 3,000 years of vegetation history has demonstrated an adaptive ability to resist these catastrophes, accounting for the long-term persistence of endemic tree species such as *Araucaria araucana* during past geologic ages in the volcanically active southern Andes [25]. The long-term impact of aboriginal burning practices on natural fire regimes in the region is not documented and remains unclear [26]

Recently, Gonzalez [27] used a dendrochronological approach to indicate that fire is the most important disturbance agent in the *Araucaria-Nothofagus* forest landscape. Dendrochronological research has been used to determine changes in fire regime (frequency, intensity and spatial pattern) and to compare the pre- and post-Euro-American settlement phase. Mean fire occurrence intervals for the Euro-American colonization period (after 1883) in central-southern Chile have a shorter frequency than during the native American phase [26,27]. Human processes as part of ecosystem functioning must be taken in account, especially because of the spatial and temporal patterns of disturbance regimes. Human disturbance is considered as an important impact factor for the stability at regional or global level and is the main cause of landscape fragmentation [26]. Coniferous forest ecosystems are good examples of cumulative effects integrating natural and anthropogenic impacts over different time scales [26]. The Chilean mountain forests show very old records of

past fire occurrence, at least for the last 600 years [26,28,29]. At those forest ecosystems, natural regeneration patterns and recovering biogeochemical processes after catastrophic disturbances are discussed as an adapted high resilience capacity [30,31].

Disturbances in forest ecosystems are of natural and anthropogenic origin, promoting the dynamics of biotic components and biogeochemical processes. In Chile, different natural and anthropogenic induced disturbances are responsible for temporal and permanent land use changes with respective impacts to the local ecosystems (Fig. 1).

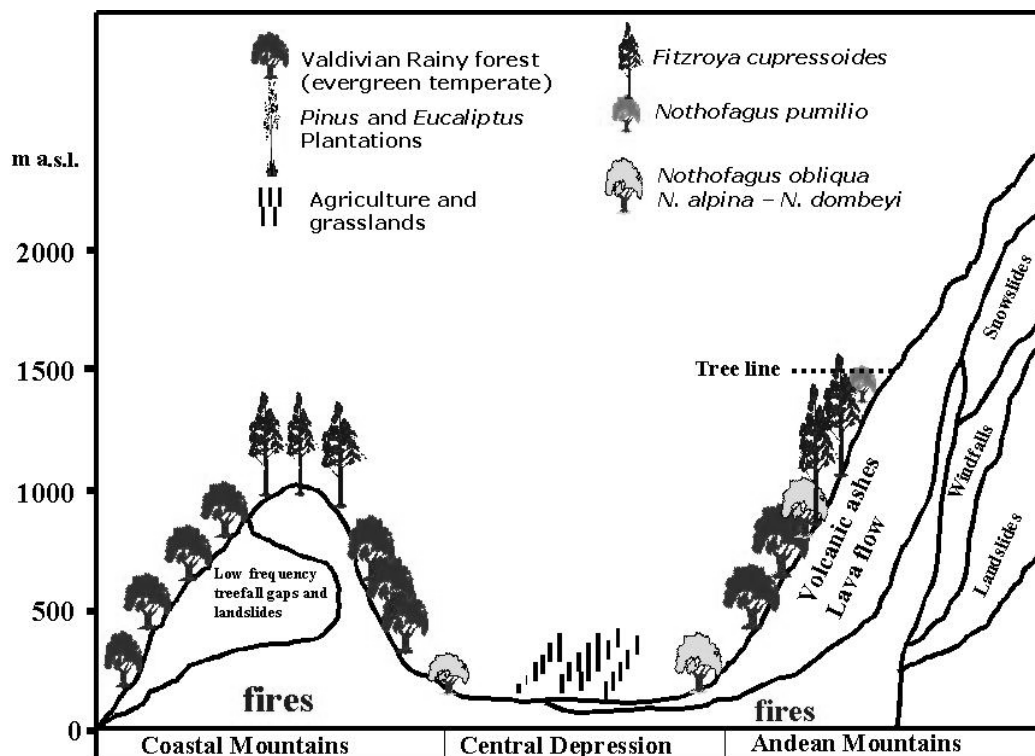


Fig. 1. Disturbances in central-southern Chile (38-42°S) on different ecosystem types (adapted from Lara *et al.* [28])

Ecosystem stability is an arbitrary concept related to fine and broad scale disturbances and their influences to biological dynamics [32]. Among its theoretic edges, the formulation of the equilibrium hypothesis could be generated, such as higher species diversity related to intermediate levels of disturbances [33]. An ecosystem in steady-state condition may be able to recover faster after a disturbance, characterizing the resilience concept [34]. The ecosystem ability to sustain its threshold disturbance is a constraint to local or global extinction risks of threatened species [35].

Fire disturbances are of great importance to plant communities. However, not all of the related hypotheses are yet cleared out [36]. Evolutionary patterns to forest communities in Chile have been explained as a consequence of wildfire events, like

Fitzroya cupressoides (Mol.) Johnst. forests on the coastal mountains [37] and *Araucaria araucana* (Mol.) K. Koch. forests in the Andean Mountains [38,29,25]. Catastrophic events of wildfire and volcanic lava flow are the most significant events that induce dynamics to *Araucaria-Nothofagus* communities in Andean mountains of Chile and Argentina [39,40]. After a wildfire in the *Araucaria-Nothofagus* ecosystem, inorganic N losses increase significantly [31]. However, a fast recovering of the conservative N flux is observed reflecting a high resilience capacity of those Andean forest ecosystems.

Fire has been a low frequency disturbance at *Araucaria-Nothofagus* ecosystems at the Andean range until about two centuries ago, but it increased after European settlements in this region [29]. It is believed that before major human influences to forest ecosystems in southern South America only natural climatic oscillations influenced fire regimes [7].

Anthropogenic land cover change in the central depression of southern Chile (40° - 42° S) is the most evident process of deforestation and agricultural expansion [41]. A large fraction of the *Nothofagus* forests in that region has been cleared for agriculture during the last century. Patches of second-growth forest cover vast areas of the regional landscape, leaving only scattered stands as a result from intensified agriculture activity [42]. Anthropogenic activities such as transport, industry and agriculture have been increasing in the central depression of this region and can substantially alter the atmospheric N load and subsequently N deposition [43]. An altitudinal transect of this area shows a wet inorganic-N deposition to have a markedly seasonal variation, with highest values occurring during spring and summer. The annual rates of wet NH_4^+ deposition range from 2.8 kg N ha⁻¹ yr⁻¹ in the Andean mountain forests to 6.4 kg N ha⁻¹ yr⁻¹ in the agricultural region around the city of Osorno [44].

Cattle pastures located in the central depression of central-southern Chile are responsible for about 70% of Chilean milk production and 45% of Chilean meat production [45]. As a consequence, substantial amounts of NH_3 can be emitted from pastures, cowsheds, dung and manure or mineral fertilizer applications, which in turn can be intercepted by the forests of the Andean Cordillera. Total ammonia emission from this region was estimated at 5.6 ton NH_3 -N yr⁻¹ [45]. It is hypothesized that dry inorganic N deposition is for about 10 times underestimated and increases in the following order of land use: *Pinus* plantation < grassland < *Nothofagus* forest [46]. Another study in southern Chile [47] reported that N retention in catchments was related with native forest coverage. However, currently, the aquatic and terrestrial N cycle is increasingly influenced by human activities [48].

With respect to soil C, Huygens *et al.* [49] indicated that the importance of land use change affected the SOC dynamics and aggregate stability by modifying soil pH, root SOC and accompanying management practices on a south Chilean Andisol.

The expansion and intensity of agricultural and livestock activities in the region suggest incorporation of technological and economic support in the near future, which will result in a significant driving force for milk and meat production. Local farmers use mineral fertilizers and manure slurries to increase pasture and crop yield. This will have a major impact on soil and can potentially pollute superficial and sub-superficial water runoffs during the winter periods. An increasing amount of atmospheric dry and wet NH_y deposition is an important indicator of a changing environmental pattern. On the other hand increased agricultural activity will also change the terrestrial trace gas (N₂O, NO, CO₂ and CH₄) budget [50]. However, currently, data from Chilean ecosystems are not yet available.

In southern-central Chile, ground water in the vicinity of agricultural and livestock farms indicate microbiological contamination (e.g. total and fecal coliforms, and *E. coli*). It usually exhibits amounts of ammonium, manganese and phosphate which are higher than the maximum levels accepted by the Chilean National Institute of Normalization for human and animal consumption [51,52]. The bacteriological quality of water does not only concern determination of the presence of pathogenic bacteria, but also the occurrence of microorganisms, which can alter the physical and chemical characteristics as a result of their metabolic activity.

4. Conclusions

Temperate forests in Chile constitute one of the most important pristine ecosystems around the world. Historical land use changes are documented for the last 13,000 yr B.P. and are associated to human settlements. Natural and anthropogenic disturbance in the region modify the dynamics of the natural vegetation and composition of the landscape. Currently, deforestation and plantation of exotic trees are the main important environmental impacts on the Chilean temperate forests. Permanent increasing agriculture activities in the central depression of southern Chile contribute to enhanced N deposition. Important questions are still to be answered concerning the C and N cycle of agro-ecosystems at the central depression of southern Chile.

Acknowledgments

This work was supported by Grants Fondecyt 1050313, 1085081 and Bilateral Project Chile-Flanders, Belgium is greatly acknowledged. The authors would like to thanks the reviewers and editors for the valuable comments. L. Paulino wishes to thank the *Programa Bicentenario de Ciencia y Tecnología*-World Bank-UdeC, Chillán, Chile.

References

- [1] C. Donoso, “Bosques templados de Chile y Argentina. Variación, estructura y dinámica”, Editorial Universitaria, Santiago, Chile. 1993.
- [2] J. Armesto, P. León, and M. Arroyo, “Los bosques templados del sur de Chile y Argentina: una isla biogeográfica”, In: J. Armesto, C. Villagrán, and M. K. Arroyo. Ecología de los bosques nativos de Chile. Editorial Universitaria, Santiago, 71-92, 1996.
- [3] M. Willson, C. Smith-Ramírez, C. Sabag, and J. Hernández, “Mutualismos entre plantas y animales en bosques templados de Chile”, In: J. Armesto, C. Villagrán, and M. K. Arroyo. Ecología de los bosques nativos de Chile. Editorial Universitaria, Santiago, 251-278, 1996.
- [4] J. Rau, “Biodiversidad y colecciones científicas”, Revista Chilena de Historia Natural, 78, 341-342, 2005.
- [5] C. Villagrán, and L. Hinojosa, “Historia de los bosques de Sudamérica”, Revista Chilena de Historia Natural, 70, 241-267, 1997.
- [6] R. Rozzi, J. Armesto, B. Goffinet, W. Buck, F. Massardo, S. Silander, M. T. K. Arroyo, S. Russell, Ch. Anderson, L. Cavieres, and J. B. Callicott, ”Changing lenses to assess biodiversity patterns of species richness in sub-Antarctic plants and implications for global conservation”, Frontiers in Ecology and the Environment, , 61, 131-137, 2008.
- [7] A. Lara, and R. Villalba, R. “A 3,620-year temperature record from *Fitzroya cupressoides* tree rings in southern South America”, Science, 260, 1104-1106, 1993.
- [8] P. Vitousek, L. Hedin, P. Matson, J. Fownes, and J. Neff, “Within-system element cycles, input-output budgets, and nutrient limitation”, in M. Pace, and P. Groffmann (Eds.). Success, limitations and frontiers in ecosystems science. Springer-Verlag, New York, 432-451, 1998.
- [9] P. Vitousek, and R. Howarth, “Nitrogen limitation on land and in the sea: How can it occur?”, Biogeochemistry, 13, 87-115, 1991.
- [10] L. Hedin, J. Armesto, and A. Johnson, “Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory”, Ecology, 76, 493-509, 1995.
- [11] S. Perakis, and L. Hedin, “Fluxes and fates of nitrogen in soil of an unpolluted old-growth temperate forest, southern Chile”, Ecology, 82, 2245-2260, 2001.
- [12] S. Perakis, and L. Hedin, “Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds”, Nature, 415, 416-419, 2002.
- [13] C. Perez, J. Armesto, C. Torrealba, and M. Carmona, “Litterfall dynamics and nitrogen use efficiency in two evergreen temperate rainforests of southern Chile”, Austral Ecology, 28, 591-600, 2003.
- [14] P. Satti, M. Mazzarino, M. Gobbi, F. Funes, L. Roselli, and H. Fernandez, “Soil N dynamics in relation to leaf litter quality and soil fertility in north-western patagonian forests”, Journal of Ecology, 91, 173-181, 2003.
- [15] G. Buamscha, M. Gobbi, M. Mazzarino, and F. Laos, F. “Indicators of nitrogen conservation in *Austrocedrus chilensis* forests along a moisture gradient in Argentina”, Forest Ecology and Management, 112, 253-261, 1998.

- [16] C. Lusk, and O. Contreras, "Foliage area and crown nitrogen turnover in temperate rain forest juvenile trees of differing shade tolerance", *Journal of Ecology*, 87, 973-983, 1999.
- [17] C. Lusk, "Leaf life spans of some conifers of the temperate forests of South America", *Revista Chilena de Historia Natural*, 74, 711-718, 2001.
- [18] D. Lipson, and T. Näsholm, "The unexpected versatility on plants: organic nitrogen use and availability in terrestrial ecosystems", *Oecologia*, 128, 305-316, 2001.
- [19] S. Perakis, J. Compton, and L. Hedin, "Nitrogen retention across a gradient of ^{15}N additions to an unpolluted temperate forest soil in Chile", *Ecology*, 86, 96-105, 2005.
- [20] D. Huygens, P. Boeckx, P. Templer, L. Paulino, O. Van Cleemput, C. Oyarzún, Ch. Müller, and R. Godoy, "Mechanisms for retention of bioavailable nitrogen in volcanic rainforest soils", *Nature Geosciences*, 1, 543-548, 2008.
- [21] T. Dillehay, and J. Rossen, "Integrity and distribution of archeological collection. Monte Verde. A late Pleistocene settlement in Chile", Vol. II. The archeological context and interpretation, T. Dillehay (ed.) Smithsonian Institution Press, 351-381, 1997.
- [22] C. Ramírez, "The Macrobotanical remains", in Monte Verde. A Late Pleistocene settlement in Chile, Vol.1. Paleoenvironment and site context. T. Dillehay (ed.) Smithsonian Institution Press, 147-170, 1989.
- [23] T. Dillehay, T. "Monte Verde. Un asentamiento humano del pleistoceno tardío en el Sur de Chile", Ediciones LOM, Serie Universitaria, Santiago de Chile, 2004.
- [24] M. Solari, C. Lehnebach, and L. Adan, "Metodologías compartidas para el estudio de carbones y semillas de los períodos Arcaico y Formativo del "Alero Marifilo 1" (Lago Calafquen, 30°Lat.S)", *Boletín Museo Nacional de Historia Natural de Chile*, 53, 125-137, 2004.
- [25] C. Heusser, J. Rabassa, A. Brandani, and R. Stuckenrath, "Late-holocene vegetation of the Andean *Araucaria* region, Province of Neuquén, Argentina", *Mountain Research and Development*, 8, 53-63, 1988.
- [26] P. Alaback, T. Veblen, C. Whitlock, A. Lara, T. Kitzberger, and R. Villalba, "Climatic and human influences on fires regimes in temperate forest ecosystems in North and South America", in G. Bradshaw, and P. Marquet, (eds.), *How landscape change – Human disturbance and ecosystem fragmentation in the Americas*, *Ecological Studies* 162, 49-87, 2003.
- [27] M. González, "Fire history data as reference information in ecological restoration", *Dendrocronologia*, 22, 149-154, 2005.
- [28] A. Lara, A. Wolodarsky-Franke, J. Aravena, M. Cortes, S. Fraver, and F. Silla, "Fire regimes and forest dynamics in the Lake Region of south-central Chile", in T. Veblen, W. Baker, G. Montenegro, and T. Swetnam (Eds.), *Fire and climatic change in temperate ecosystems of the western Americas*, *Ecological Studies*, Springer, New York, 160, 322-342, 2003.
- [29] M. González, T. Veblen, and J. Sibold, "Fire history of *Araucaria-Nothofagus* forests in Villarrica National Park, Chile", *Journal of Biogeography*, 32, 1187-1202, 2005.

- [30] P. Boeckx, L. Paulino, C. Oyarzún, O. Van Cleemput, and R. Godoy, "Soil $\delta^{15}\text{N}$ patterns in old-growth forests of southern Chile as integrator for N cycling", *Isotopes in Environmental and Health Studies*, 41(3), 249-259, 2005.
- [31] L. Paulino, "Efectos post-incendio sobre el ecosistema *Araucaria-Nothofagus*, Parque Nacional Tolhuaca", Tesis de Doctorado en Ciencias, Mención Sistemática y Ecología, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile, 2006.
- [32] P. Morin, "Community Ecology", Blackwell, 303-338, 1999.
- [33] J. Connell, "Diversity in tropical rainforests and coral reefs", *Science*, 199, 1302-1310, 1978.
- [34] F. Bormann, and G. Likens, "Patterns and processes in a forested ecosystem", Springer, New York, 1994.
- [35] H. Akçakaya, M. Burgman, and L. Ginzburg, "Applied population ecology", Applied Biomathematics, New York, 1997.
- [36] R. Daubenmire, "Ecología vegetal", Limusa, México, 383-403, 2001.
- [37] A. Lara, S. Fraver, J. Aravena, and A. Wolodarsky-Frane, "Fire and the dynamics of *Fitzroya cupressoides* (alerce) forests of Chile's Cordillera Pelada", *Ecoscience*, 6, 100-109, 1999.
- [38] S. Bekessy, A. Lara, M. González, M. Cortes, A. Premoli, and A. Newton, "Variación en *Araucaria araucana* (Molina) K. Koch (*Araucaria* o Pehuén)", in C. Donoso, A. Premoli, L. Gallo, and R. Ipinza (Eds.), Variación intraespecífica en las especies arbóreas de los bosques templados de Chile y Argentina, Editorial Universitaria, Santiago, 215-232, 2004.
- [39] B. Burns, "Fire-induced dynamics of *Araucaria araucana-Nothofagus antarctica* forest in the southern Andes", *Journal of Biogeography*, 20, 669-685, 1993.
- [40] T. Veblen, J. Armesto, R. Burns, T. Kitzberger, A. Lara, B. Leon, and K. Young, "The coniferous forests of South America", in F. Andersson (Ed.), Coniferous Forests Ecosystems of the World, Series Elsevier, Brussels, 6, 293-317, 2005.
- [41] E. Neira, H. Verscheure, and C. Revenga, "Chile's frontier forests, conserving a global treasure, Global Forest Watch, WRI, Washington, 2002.
- [42] T. Veblen, C. Donoso, T. Kitzberger, and A. Robertus, A. "Ecology of southern Chilean and Argentinean *Nothofagus* forests", in The ecology and biogeography of *Nothofagus* forests (eds. T. Veblen, R. Hill and J. Read), Yale University Press, 293-353, 1996.
- [43] R. Godoy, L. Paulino, C. Oyarzún, and P. Boeckx, "Atmospheric N deposition in Central and Southern Chile. An overview", *Gayana Botanica*, 60, 47-53, 2003.
- [44] C. Oyarzún, R. Godoy, and S. Leiva, "Deposición atmosférica de nitrógeno en un transecto valle longitudinal-Cordillera de los Andes, centro-sur de Chile", *Revista Chilena de Historia Natural*, 75, 233-243, 2002.
- [45] F. Salazar, J. Dumont, M. Santana, B. Pain, D. Chadwick, and E. Owen, "Prospección del manejo y utilización de afluentes de lecherías en el sur de Chile", *Archivos de Medicina Veterinaria*, 35, 215-225, 2003.

- [46] R. Godoy, J. Haneke, J. Staelens, C. Oyarzún, L. Paulino, and M. Barrientos, "Dry deposition of nitrogen to passive samplers in grassland and forest canopies in the central depression of southern Chile", *Gayana Botanica*, 62, 110-119, 2005.
- [47] C. Oyarzún, C. Aracena, P. Rutherford, R. Godoy, and A. Deschrijver, "Effect of land use conversion from native forests to exotic plantations on stream water quality in southern Chile", *Water, Air & Soil Pollution*, 179, 341-350, 2007.
- [48] L. Hedin, L. Granat, G. Likens, T. Buishand, J. Galloway, T. Butler, and H. Rodhe, "Steep declines in atmospheric base cations in regions of Europe and North America", *Nature*, 367, 351-354, 1994.
- [49] D. Huygens, P. Boeckx, O. Van Cleemput, R. Godoy, and C. Oyarzún, "Aggregate structure and stability linked to carbon dynamic in a Chilean Andisol", *Biogeosciences*, 2, 203-238, 2005.
- [50] O. Van Cleemput, and P. Boeckx, "Alteration of nitrogen cycling by agricultural activities, and its environmental and health consequences", *Gayana Botanica*, 62, 98-109, 2005.
- [51] Instituto Nacional de Normalización de Chile, "Calidad del agua-muestreo: parte II: guía para el maestro de aguas subterráneas (Water quality-sampling. Part II: Guidance on sampling of groundwaters)", Santiago, 1998.
- [52] J. Nissen, M. Garay, A. Aguilera, and E. Valenzuela, "Calidad de las aguas subterráneas de la Décima Región de Chile", *Agro Sur*, 28(1), 25-39, 2000.

Leaf litter dynamics in headwater streams of the Chilean Andes: influence of shredders and silvicultural activities

Giovany Guevara¹, Roberto Godoy², Pascal Boeckx³, Carlos Jara¹, Carlos Oyarzún⁴

¹ Instituto de Zoología, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: giovany.guevara@postgrado.uach.cl – cjara@uach.cl

² Instituto de Botánica, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: rgodoy@uach.cl

³ Laboratory of Applied Physical Chemistry – ISOFYS, Ghent University, Coupure links
653, B-9000 Ghent, Belgium, Email: pascal.boeckx@ugent.be

⁴ Instituto de Geociencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: coyarzun@uach.cl

Abstract. Leaf litter dynamic processes (input and decomposition) were evaluated in evergreen (pristine and managed) and secondary deciduous forested streams in the Andes of southern Chile (40°S). The purpose was: (a) to determine the effect of forest management practices on litter yield from riparian areas and their importance for associated stream channels, (b) to compare litter decomposition processes among single and mixed leaf litter, and (c) to establish the importance of leaf-eating aquatic invertebrates (shredders) on the litter disappearance after two months of incubation in each stream. Litter fall input was evaluated from December 2006 to November 2007, with results as follow: 4173, 3377 and 3166 kg ha⁻¹ yr⁻¹ for the deciduous, managed and pristine forest streams, respectively. In the mixed litter assay with coarse bags (summer 2007), the abundance of plecopteran, trichopteran and dipteran shredders was higher in the evergreen pristine stream followed by deciduous and the evergreen managed forest stream, respectively. These abundances were concomitant with the decomposition rates in the evergreen forest streams ($k = -0.0091$ and -0.0049 day⁻¹, respectively). The second experiment (with coarse and fine bags, autumn 2007) accounted for a higher decomposition rate of *Laureliopsis philippiana* in the pristine ($k = -0.0120$ day⁻¹) than the managed stream (-0.0049 day⁻¹). During both sampling periods, k values for *Nothofagus alpina* were highest, evidenced mainly in the summer (*ca.* 1.5 times) and into coarse-litter bags ($k = -0.0289$ vs. -0.0047 day⁻¹). The effect of forestry activities on the organic matter fluxes and shredder assemblages in the headwater Andean streams of South-Central Chile is discussed.

1. Introduction

Running water ecosystems encompass a wide spectrum of habitats, flowing continuously from small mountain springs, then mid-order streams that downstream

create large lowland rivers which finally join to the sea [1]. Headwater streams *i.e.*, first- or second-order streams, which comprise upwards of 70% of the lotic network within a watershed [2], are often strongly influenced by adjacent land [3,4]. Low-order streams in forested catchments are heterotrophic with food webs dependent on inputs of organic matter from surrounding areas [5,6]. They are sites of input, storage, transformation and subsequent export of detritus to downstream reaches [7]. In addition, small streams are physically heterogeneous ecosystems consisting of a diverse assemblage of hydraulic habitats, associated environmental variables and biotic communities [8,9]. Production of both primary and secondary consumers in headwater streams is tightly linked to the supply of leaf litter from the riparian forest [10]. Leaf litter from riparian and corridor vegetation forms the vital energy input into the streams as coarse particulate organic matter (CPOM) [11]. Soon after leaves enter the streams, they are rapidly colonised by aquatic microbes and also by invertebrates, especially shredders [12]. Although fragmentation can occur by physical forces and invertebrate feeding, other processes also occur simultaneously, with variation in the relative contribution of each [13]. Shredders have therefore the potential to accelerate leaf litter decomposition [14,15]. One widely used method to assess the role of invertebrates on leaf breakdown is the use of coarse meshed (~5mm) and fine meshed (~0.5mm) litter bags (*sensu* [16]). Rates of breakdown are typically determined by placing known amounts of leaf litter in packs or mesh bags in a stream and periodically determining leaf mass losses [17]. The results of such experiments have been contradicting, mainly related to differences in both litter quality and invertebrate densities in streams [18].

The ecological role of allochthonous leaf litter as principal source of energy in forested streams of temperate areas in Europe, North America and New Zealand has been well documented [19], with more than 79% of studies for the period 1996-1997 [16]. However, despite the importance of leaf litter in stream ecosystems, studies on litter decomposition in South American temperate areas, are scarce [20,21]. Mountain lotic systems have an intimate contact with their surrounding catchments and the terrestrial ecosystems they contain. Thus the trophic dynamics of many low-order streams, for example, is driven primarily by inputs of terrestrial organic matter. Likewise, these small streams are vulnerable to human alteration of the catchment, riparian zone, and channel [22-24]. Silvicultural management practices impact the soil productivity and the magnitude of primary effects depend of forest type, soil, topography and climate, which alter energetic linkages between aquatic and terrestrial habitats in forested small streams, can affect associated ecosystem processes [25]. Forestry activities executed near to stream channels have the potential to affect litter fall input, increase amounts of light, discharge, and sediment runoff, modify the supply of basal resources, changes in the supply of large wood, temperature modifications, and food-web effects [26-28].

South-Central Chile is blessed with diverse freshwater habitats [29] that include several streams and rivers, originating from both Coastal and Andean Cordilleras. However, from an ecological point of view, the majority of these aquatic systems are understudied or unexplored [30], especially those located in Andean remote

areas. Therefore, information on leaf litter dynamics in streams would be of practical importance towards our comprehension of trophic dynamics of the southern temperate forest streams. The effect of different riparian vegetation composition (native vs. exotic) on colonization by invertebrates and decomposition has been reported in Chile by Valdovinos [20]. However, it is the first time that the effects of different land-management regimes in native forest on quantities of litter fall actually entering streams and its decomposition in headwater Andean streams, is reported. Such information is needed to properly assess the strength of the link between riparian organic matter supplies and in-stream food webs. Thus, the objectives of this study were: (a) to assess the influence of shredders on leaf litter decomposition of mixed leaves obtained from the riparian forests and incubated into coarse mesh bags in different forested low-order streams (pristine, managed and deciduous), (b) to establish the leaf mass losses and decomposition rates for three common evergreen and one deciduous plant species using coarse and fine mesh bags in the same contrasting headwater streams in the Andean cordillera of South-Central Chile. Further, we linked the effect of forestry activities on shredders richness and litter decomposition rates.

2. Material and Methods

2.1 Study Area

We selected three low-order streams located in the San Pablo de Tregua experimental area, in the Andean mountain, South-Central Chile (39°S, 72°W). We studied two contrasting evergreen forested streams (natural vs. silviculturally managed), both with riparian vegetation composed by *Myrceugenia planipes* (H. et A.) Berg, *Laureliopsis phillipiana* Looser and *Saxegothea conspicua* Lindl. One third stream with secondary deciduous forest composed by *Nothofagus alpina* (P. et E.) Oerst, was also selected. More detailed information concerning this area and its silvicultural management is reported in [31-36].

2.2 Sampling and data analysis

2.2.1 Experimental trial 1. Decomposition of litter mixtures into coarse litter bags (summer 2007)

Randomly dry mixed evergreen and single deciduous material (10 g) was placed into separate litter bags (20 x 20 cm, 5mm mesh size), during 60 days and recovered after 3, 7, 15, 30, 45 and 60 days exposure time, in pristine, managed and deciduous forest streams, respectively. Laboratory analyses were carried out following the methodology proposed by [37]. Aquatic insects (and other invertebrates), nymphs and larvae, associated with the remnant leaf litter at each sampling date, were removed by hand and sorted as shredders and non-shredders.

2.2.2 Experimental trial 2. Decomposition of single leaf material into coarse- and fine-meshed bags (autumn 2007)

Individual organic material (10 g) was incubated in coarse (5mm) and fine (0.5mm) nylon bags and recovered following the same procedure as above. In December 2008, we sampled (Surber sampler 0.30 m²; 250 µm mesh) a 120-m reach of each stream for evaluation of the invertebrate population, potentially associated to leaf litter disappearance. The “real” colonization data were unfortunately lost during the catastrophic fire in the laboratory (03.12.2007).

We also registered the riparian litter fall input from December 2006 to November 2007 using litter traps (50 x 50 cm), set up at 1 m above ground level near the stream channels. Decomposition rates were obtained from the exponential decay model $W_t = W_0 e^{-kt}$ [38] and the percentage of leaf mass loss per plant species was also quantified. Comparison of litter fall input among streams was performed with a two-way ANOVA (factors: forest stream and season) and, decomposition rates was compared by analysis of covariance (ANCOVA, time as covariate) [39]. All analyses were performed using STATISTICA 7 and the level of significance was set at 0.05.

3. Results and discussion

3.1 Seasonal litter fall input

The greatest litter fall mass was collected during autumn and winter. Overall, it was higher for the deciduous riparian forest followed by the managed and pristine forests (Fig. 1). No significant differences were noted between the deciduous and the contrasting evergreen forests (ANOVA, $F_{2, 24} = 0.104$, $P = 0.901$), but among seasons ($F_{3, 24} = 7.099$, $P = 0.001$). During spring less litter fall input was noted for all forests. The annual foliar litter fall biomass inputs to stream channels for the pristine, managed and deciduous forests were respectively 3166, 3377, and 4173 kg ha⁻¹ yr⁻¹. Litter fall input behaviour was similar to the recorded behaviour for other Chilean temperate rainforests [40,41], but the biomass was lower than that recorded for the deciduous congener *Nothofagus obliqua* (Mirb.) Oerst (central depression) and for the evergreen *N. betuloides* (Mirb.) Oerst in the Antillanca Valley (Chilean Andes, 40°S) [42].

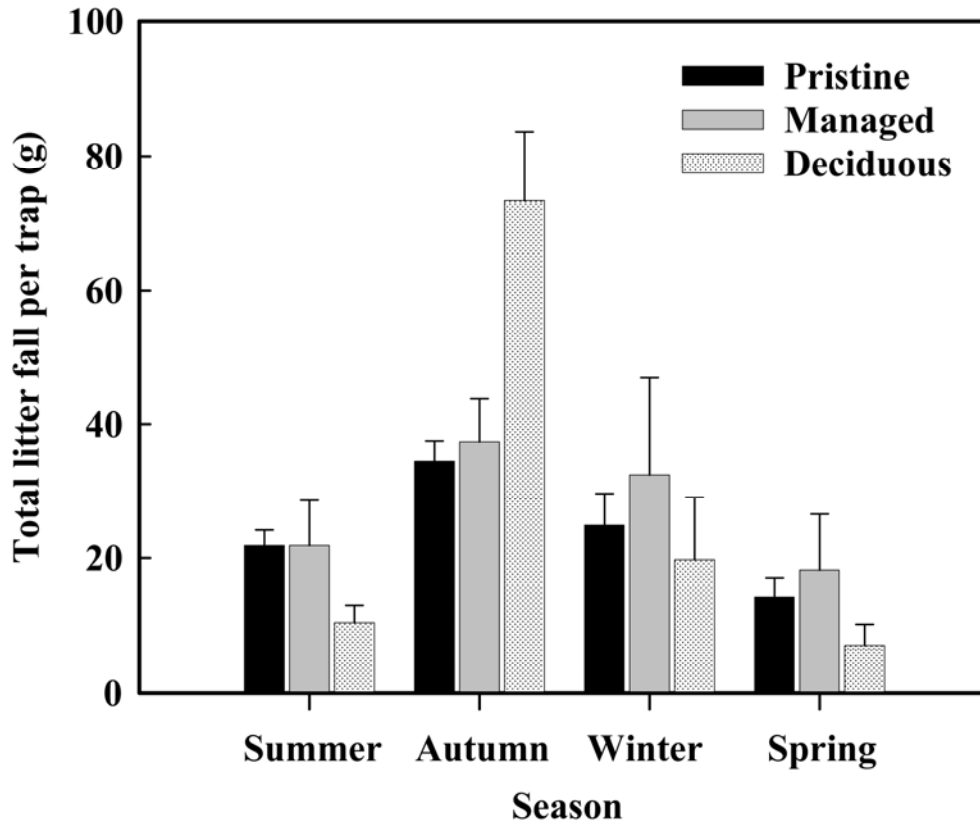


Fig. 1. Litter fall input per trap (mean \pm SE) and per season from three contrasting riparian forests in the Andean mountain, South-Central Chile from December 2006 to November 2007. Both pristine and managed riparian forests are evergreen

3.2 Mixed leaf species and associated decomposer invertebrates

Considering the exponential decay model obtained from the percentage of dry mass remaining over time, the decay rate of deciduous leaf species was higher ($k = -0.0413 \text{ day}^{-1}$) than the rate for both mixed leaves of the pristine (-0.0091 day^{-1}) and managed (-0.0049 day^{-1}) forest streams. The mass of leaves remaining at the end of the experiment (after 60 days) was 11% of the original mass for the deciduous forest stream, 58% for the pristine and 68% for the managed forest streams (Fig. 2a). The analysis of leaf decomposition standardised per day yielded significant differences among forested streams (ANCOVA, $F_{2, 15} = 1.09$, $P = 0.002$) with k values ranging as follow: deciduous > pristine > managed (Fig. 2b). It is important to highlight that leaf diversity can affect the process of decomposition and hence, to separate the contribution of single species in the mixtures. Some interactive effects (e.g. decomposition of a species is enhanced while another one is retarded in the mixtures) can only be detected as an overall additive response [43].

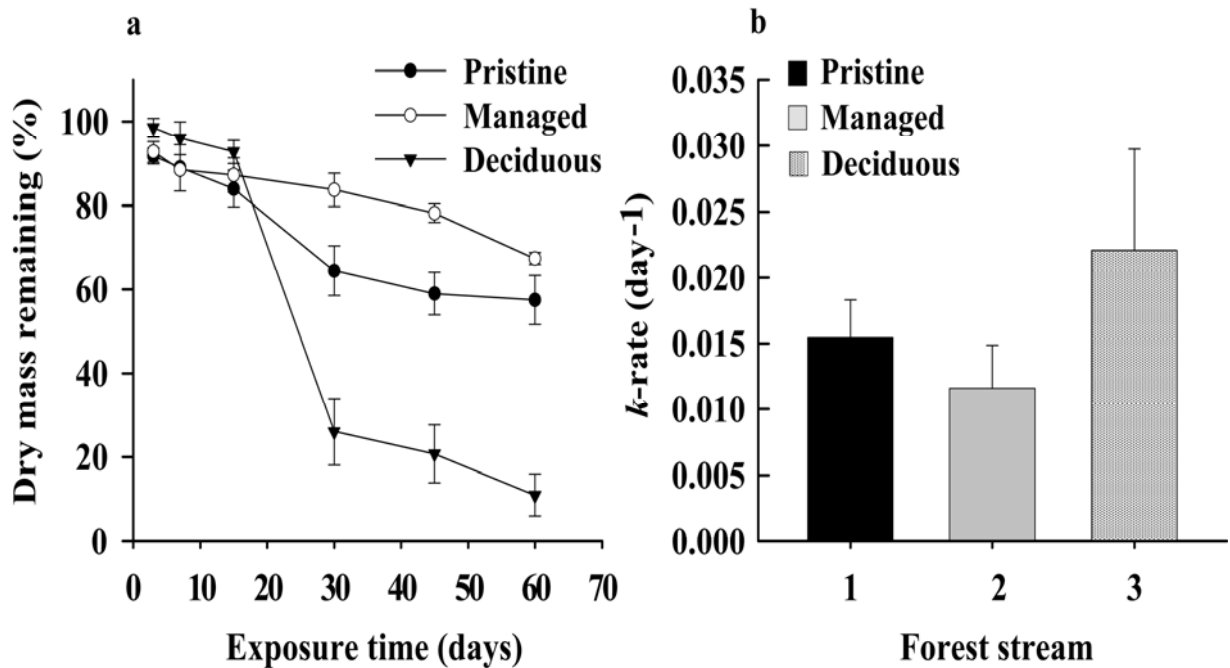


Fig. 2. Leaf mass loss (a) and decomposition rate (b) of mixed leaves incubated in coarse bags in contrasting forest streams in the Andean mountain, South-Central Chile during summer 2007. Values indicate mean \pm SE

The associated fauna with leaf bags was similar among streams but with marked differences in its abundance. As expected, in the bags, shredders were more abundant than non-shredders (Fig. 3). The pristine forest stream revealed a higher abundance of Plecoptera, Ephemeroptera and Nematomorpha, but had a lower density of Diptera. Considering only the shredder fauna, it seems that the Plecoptera assemblage dominates in the pristine forest stream, Trichoptera in the deciduous and Diptera in the managed forest stream. However, leaf-eating trichopterans and plecopterans in the deciduous forest stream showed slight differences, and Plecoptera was also an important component in the managed stream (Fig. 3a). Non-shredder invertebrates were represented mainly by Ephemeroptera (Fig. 3b). Within shredding invertebrates, plecopterans and trichopterans were the most important taxa presents on decomposing leaves in Andean streams [20,21], more than dipterans and/or crustaceans, as reported for other temperate zones worldwide [16]. The effect of forestry activities on litter decomposition might reflect changes in the composition of benthic invertebrates [44]. It has been observed that enhancement of mass loss in mixed litter bags correspond with a higher arthropod abundance in both soil [45] and water [18,46] systems.

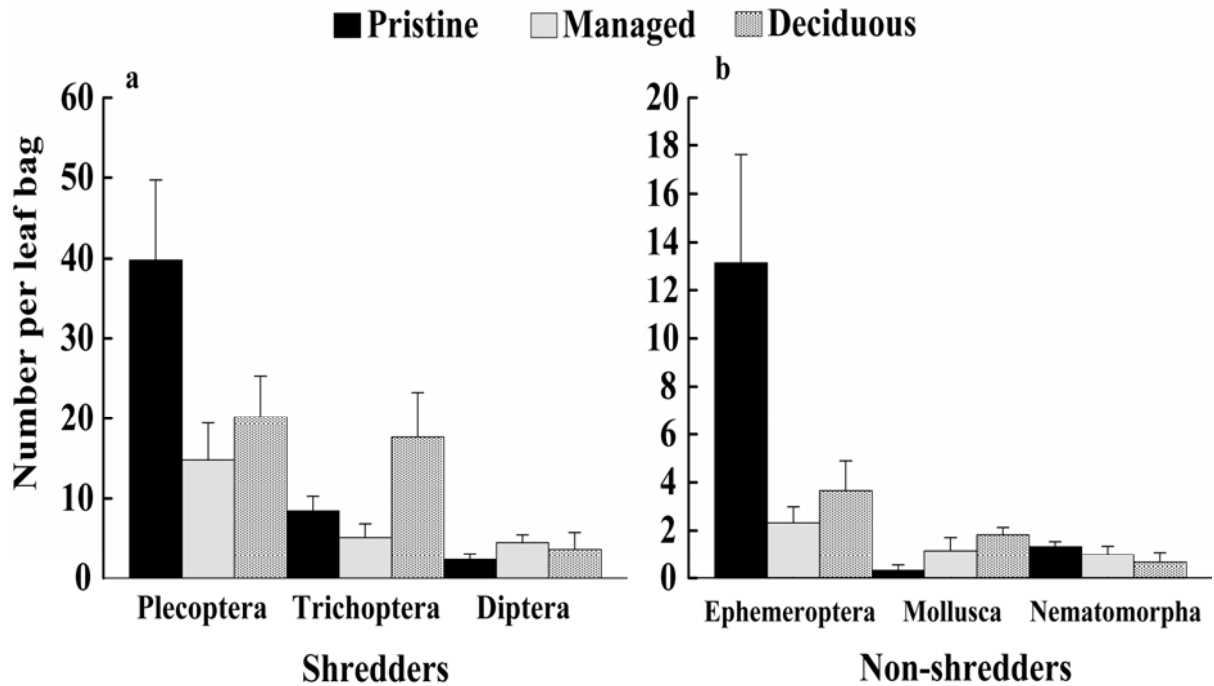


Fig. 3. Abundance of major taxa registered in coarse bags with a mixture of leaf litter in contrasting forest streams in the Andean mountain, South-Central Chile. Note the differing Y-axes: **a**. Leaf-eating invertebrates, **b**. Non-shredders. Data pooled across all time of immersion. Abundance is expressed as mean number of individuals per leaf bag. Pristine and managed forested streams are evergreen. Bars indicate the SE of the mean.

3.3 Single leaf species and the effect of bag mesh size and forestry activities

Globally, the decay rates varied ($k \text{ days}^{-1}$) between a maximum k value of $-0.0369 \pm 0.0029 \text{ day}^{-1}$, recorded in the deciduous forest stream in the coarse bags, and a minimum k value of $-0.0100 \pm 0.0026 \text{ day}^{-1}$, recorded in the managed forest stream in fine bags (Fig. 4). The decomposition rate and leaf mass loss was faster for *Nothofagus alpina* followed by *Laureliopsis philippiana*, *Myrceugenia planipes* and *Saxegothaea conspicua* (Table I). There was a consistent reduction in the breakdown rates of leaves species in the fine bags for the three streams, with the exception of *M. planipes*.

Overall, among streams, decomposition rates were lower in the managed than in the pristine forest stream. Decomposition rates of single leaf species were markedly different, with deciduous leaves decomposing faster and decay rates for evergreen leaves depending on species. As expected, leaves incubated in coarse bags lost more biomass than in fine bags, revealing significant differences in the pristine evergreen forested stream with the exception of *S. conspicua*. Nevertheless, only the decomposition rate of *L. philippiana* showed significant differences between streams, although leaves immersed in the pristine stream tended to loss more mass than in the managed stream (Table I). It is well documented that breakdown rates vary within and among leaf species [47-50] according to the physical and chemical

properties of leaves [16]. The effect of forest management and nutrient analysis of our considered evergreen tree species *L. philippiana* and *M. planipes* has been evaluated by Pérez *et al.* [51] for forests of the Chiloé Island (southern Chile). However, up till now there are no published studies on streams and on nutrient analysis of decomposing leaves of our selected tree species. This information is necessary to complement the study of the effect of forestry management on Andean in-stream organic matter fluxes.

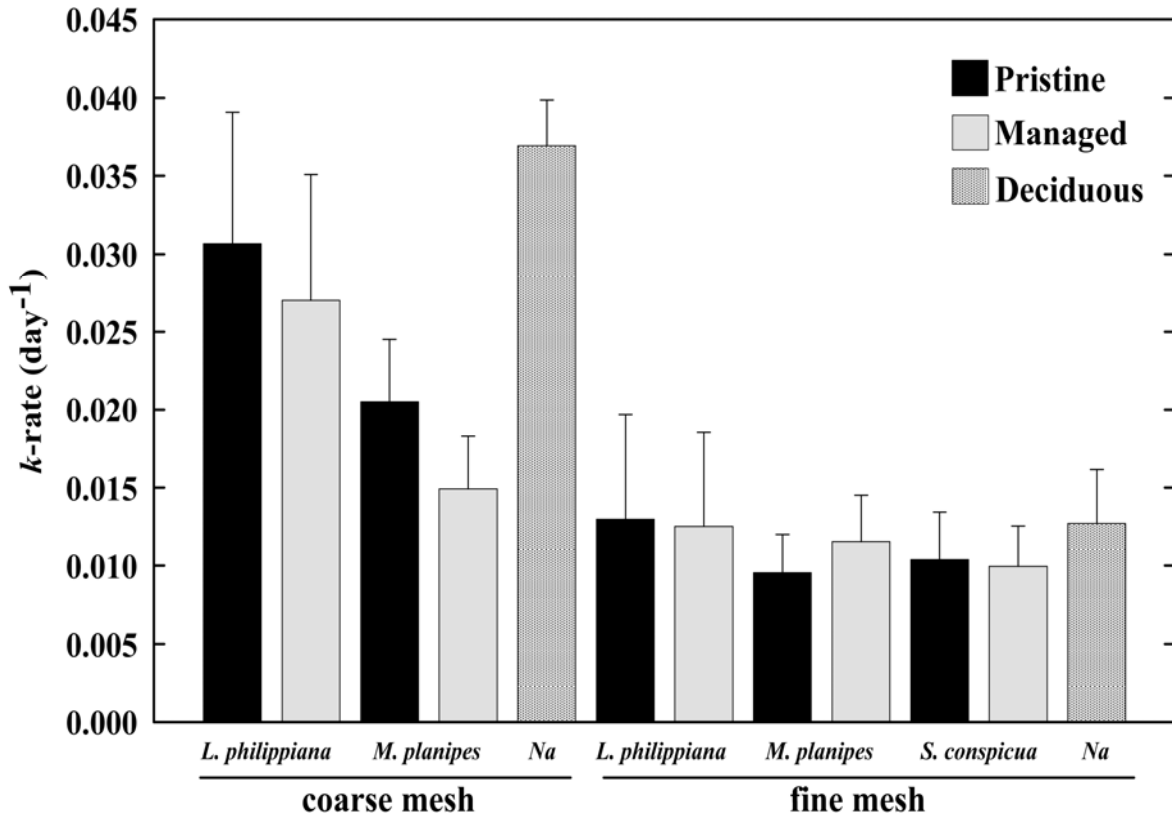


Fig. 4. Effects of silvicultural management and leaf species on mean (\pm SE) leaf litter decomposition rates in the coarse and fine mesh bags during autumn 2007 in the Andean mountain, South-Central Chile. Evergreen tree species = *Laureliopsis philippiana*, *Myrceugenia planipes*, *Saxegothaea conspicua*; deciduous tree = *Na* = *Nothofagus alpina*.

Table I. Exponential decay model, total dry mass loss, and comparison between bag mesh sizes and forest streams for four common riparian plant species, in the Andean mountain, South-Central Chile during autumn 2007

Plant species	Habitat type	Bag Mesh	Decay model	TML (%)	ANCOVA			
					$F(1, 45)$	P^w	$F(1, 45)$	P^b
<i>Laureliopsis philippiana</i>	Pristine	Coarse	$W_t = 9.247e^{-0.0120t}$	59	24.95	< 0.001	22.91	< 0.001
		Fine	$W_t = 9.105e^{-0.0038t}$	27				
	Managed	Coarse	$W_t = 8.794e^{-0.0049t}$	33		ns		
		Fine	$W_t = 9.183e^{-0.0036t}$	24				
<i>Myrceugenia planipes</i>	Pristine	Coarse	$W_t = 7.478e^{-0.0072t}$	51	23.08	< 0.001		Ns
		Fine	$W_t = 8.176e^{-0.0036t}$	33				
	Managed	Coarse	$W_t = 7.422e^{-0.0043t}$	40		ns		
		Fine	$W_t = 7.904e^{-0.0043t}$	36				
<i>Saxegothea conspicua</i>	Pristine	Fine	$W_t = 9.152e^{-0.0024t}$	21				Ns
	Managed	Fine	$W_t = 9.090e^{-0.0023t}$	19				
<i>Nothofagus alpina</i>	Deciduous	Coarse	$W_t = 12.00e^{-0.0289t}$	86	26.15	< 0.001		
		Fine	$W_t = 9.351e^{-0.0047t}$	33				

TML = total mass loss after 60 days immersion. P^w = probability for bag mesh size comparison within streams; P^b = probability for between streams comparison. Overall ANCOVA comparison were adjusted by the Bonferroni correction; ns = not significant

For the Surber sampling (December 2008), the richness of invertebrate taxa was higher in the secondary deciduous (16) than pristine (14) and managed (11) forest stream. Considering all forested streams, gatherers belonging to the Ephemeroptera and Diptera order, were the most abundant ones. However, in all streams, leaf-eating invertebrates (shredders) were relatively more abundant than other functional feeding groups: 50% in the pristine followed by deciduous (38%) and managed (36%). Predator insects such as *Aeshna* sp. (Odonata: Aeshnidae) and *Sialis* sp. (Megaloptera: Sialidae) were common for the Surber replicate samples of the managed stream, suggesting an additional (predation) effect on less shredder colonization and hence slower decomposition rates as observed in this disturbed stream in comparison with the pristine stream. Overall, the above mentioned results indicate that riparian forest management can have an effect on invertebrate assemblages and consequently on their contribution to the aquatic food web dynamics of low-order streams in mountain areas [52-54]. Nevertheless, further research is necessary to assess the relative importance of shredding invertebrates, since more biomass is generally associated with more rapid leaf mass loss [55].

4. Preliminary conclusions and perspectives

Breakdown rates in the managed stream were consistently lower than in the pristine and deciduous streams in both experimental trials (mixed and single leaf species treatments). This illustrates that forestry activity can have a marked impact on

ecosystem function in Andean low-order streams. Further analysis of the results is necessary to determine the usefulness of the decomposition rates in assessing the effect of forest management practices on ecosystem functioning from these freshwater systems.

Our results support the idea that decomposition of litter mixtures (compared to single species) is primarily driven by litter quality and environmental factors (both intrinsic and extrinsic), rather than by leaf species richness *per se*. However, further analysis is required to detect the effect of physical and chemical properties of the considered leaves on decomposition rates and invertebrate colonization over time. Likewise, the effect of other biotic (microorganisms and biofouling), physical and chemical variables, discharge, water temperature and pH on litter fall decomposition should be explored in each forest stream.

Acknowledgements

This project was partially funded by following grants: DIDUACH (D-2007-05), RLB (Tyler Prize for Environmental Achievement 2004), and CONICYT (AT-24080035). G. Guevara thanks the Universidad Austral de Chile for the MECESUP (UCO0214) scholarship and to Dr. Niko Verhoest headperson of the Bilateral Project Chile - Flanders by the support during a short stay in the Laboratory of Applied Physical Chemistry, Ghent University (Belgium). We are grateful to C. Aguilera who assisted us during the field work. The authors like special acknowledgements to Prof. Dr. O. Van Cleemput for the revision and useful comments in the MS.

References

- [1] B. Malmqvist, and S. Rundle, "Threats to the running water ecosystem of the world". *Environmental Conservation*, 29(2), 134-153, 2000.
- [2] R.K. Adams, and J.A. Spotila, "The form and function of headwater streams based on field and modeling investigations in the southern Appalachian Mountains". *Earth Surface Processes and Landforms*, 30(12), 1521-1546, 2005.
- [3] J.J. Rykken, A.R. Moldenke, and D.H. Olson, "Headwater Riparian forest-floor invertebrate communities associated with alternative forest management practices". *Ecological Applications*, 17(4), 1168-1183, 2007.
- [4] L.H. MacDonald, and D. Coe, "Influence of Headwater Streams on Downstream Reaches in Forested Areas". *Forest Science*, 53(148-168, 2007.
- [5] J.L. Meyer, and J.B. Wallace, "Lost linkages and lotic ecology: rediscovering small streams", in *Ecology: achievement and challenge*, Blackwell Science. Oxford, UK, 295-317, 2001.
- [6] R.L. Vannote, G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing, "The river continuum concept". *Canadian Journal of Fisheries and Aquatic Sciences*, 37(1), 130-137, 1980.

- [7] P.E. Bigelow, L.E. Benda, D.J. Miller and K.M. Burnett, "On Debris Flows, River Networks, and the Spatial Structure of Channel Morphology". *Forest Science*, 53(2), 220-238, 2007.
- [8] W.H. Lowe and G.E. Likens, "Moving Headwater Streams to the Head of the Class". *Bioscience*, 55(3), 196-197, 2005.
- [9] W.H. Lowe, G.E. Likens and M.E. Power, "Linking Scales in Stream Ecology". *Bioscience*, 56(7), 591-597, 2006.
- [10] A.C. Benke and A.D. Huryn, "Secondary production of macroinvertebrates", in *Methods in Stream Ecology*, Academic Press. San Diego, 691-710, 2006.
- [11] E.F. Benfield, "Decomposition of leaf material", in *Methods in Stream Ecology*, Academic Press. San Diego, California, 711-720, 2006.
- [12] K.W. Cummins, M.A. Wilzbach, D.M. Gates, J.B. Perry and W.B. Taliaferro, "Shredders and riparian vegetation". *Bioscience*, 39(1), 24-30, 1989.
- [13] M. Abelho, "Effects of Leaf Litter Species on Macroinvertebrate Colonization during Decomposition in a Portuguese Stream". *International Review of Hydrobiology*, 93(3), 358-371, 2008.
- [14] M.A.S. Graça and C. Canhoto, "Leaf litter processing in low order streams". *Limnetica*, 25(1-10), 2006.
- [15] M.A.S. Graça, R.C.F. Ferreira and C.N. Coimbra, "Litter processing along a stream gradient: the role of invertebrates and decomposers". *Journal of the North American Benthological Society*, 20(3), 408-420, 2001.
- [16] M.A.S. Graça, "II. Leaf Litter Processing and Invertebrates. The Role of Invertebrates on Leaf Litter Decomposition in Streams - a Review". *International Review of Hydrobiology*, 86(4-5), 383-393, 2001.
- [17] K.F. Suberkropp, "Microorganisms and organic matter decomposition", in *River Ecology and Management: lessons from the Pacific Coastal Ecoregion*, Springer. New York, 120-143, 1998.
- [18] C.J. LeRoy and J.C. Marks, "Litter quality, stream characteristics and litter diversity influence decomposition rates and macroinvertebrates". *Freshwater Biology*, 51(4), 605-617, 2006.
- [19] M. Abelho, "From litterfall to breakdown in streams: a review". *TheScientificWorld*, 1(1), 656-680, 2001.
- [20] C. Valdovinos, "Riparian leaf litter processing by benthic macroinvertebrates in a woodland stream of central Chile". *Revista Chilena de Historia Natural*, 74(2), 445-453, 2001.
- [21] R.J. Albariño and E.G. Balseiro, "Leaf litter breakdown in Patagonian streams: native versus exotic trees and the effect of invertebrate size". *Aquatic Conservation: Marine and Freshwater Ecosystems*, 12(2), 181-192, 2002.
- [22] L. Benda, D. Miller, K. Andras, P. Bigelow, *et al.*, "NetMap: A New Tool in Support of Watershed Science and Resource Management". *Forest Science*, 53(2), 206-219, 2007.
- [23] P.W. Adams, "Policy and Management for Headwater Streams in the Pacific Northwest: Synthesis and Reflection". *Forest Science*, 53(2), 104-118, 2007.

- [24] J.S. Richardson and R.J. Danehy, "A Synthesis of the Ecology of Headwater Streams and their Riparian Zones in Temperate Forests". *Forest Science*, 53(131-147), 2007.
- [25] E.D. Edwards and A.D. Huryn, "Effect of riparian land use on contributions of terrestrial invertebrates to streams". *Hydrobiologia*, 337(1), 151-159, 1996.
- [26] J.S. Richardson, "Aquatic arthropods and forestry: effects of large-scale land use on aquatic systems in Nearctic temperate regions". *Canadian Entomologist*, 140(4), 495-509, 2008.
- [27] J.R. Webster, E.F. Benfield, D.J. D'Angelo and G.T. Peters, "Effects of forest disturbance on particulate organic matter budgets of small streams". *Journal of the North American Benthological Society*, 9(2), 120-140, 1990.
- [28] M.A. Hassan, M. Church, T.E. Lisle, F. Brardinoni, *et al.*, "Sediment transport and channel morphology of small, forested streams". *Journal of the American Water Resources Association*, 41(4), 853-876, 2005.
- [29] C. Ramírez and C. San Martín, "Ecosistemas Dulceacuicolas", in *Biodiversidad de Chile: patrimonio y desafíos*, Ocho Libros Editores. Santiago, 112-125, 2006.
- [30] C. Valdovinos, "Invertebrados Dulceacuicolas", in *Biodiversidad de Chile: patrimonio y desafíos*, Ocho Libros Editores. Santiago, 204-226, 2006.
- [31] A.C. Newton, C. Echeverría, M. Gonzalez-Espinosa, B. Williams-Linera, *et al.*, "Testing forest biodiversity indicators by assessing anthropogenic impacts along disturbance gradients", in *Biodiversity loss and conservation in fragmented forest landscapes: the forest of montane Mexico and temperate South America*, CAB International, 276-290, 2007.
- [32] P.J. Donoso and C.H. Lusk, "Differential effects of emergent *Nothofagus dombeyi* on growth and basal area of canopy species in an old-growth temperate rainforest". *Journal of Vegetation Science*, 18(5), 675-684, 2007.
- [33] B.C. Schlegel and P.J. Donoso, "Effects of forest type and stand structure on coarse woody debris in old-growth rainforests in the Valdivian Andes, south-central Chile". *Forest Ecology and Management*, 255(5-6), 1906-1914, 2008.
- [34] T.T. Veblen, C. Donoso, T. Kitzberger and A. Robertus, "Ecology of southern Chilean and Argentinean *Nothofagus* forest", in *The ecology and biogeography of Nothofagus forest*, Yale University Press. Yale, 293-353, 1996.
- [35] Y. Redel, R. Rubio, R. Godoy and F. Borie, "Phosphorus fractions and phosphatase activity in an Andisol under different forest ecosystems". *Geoderma*, 145(3-4), 216-221, 2008.
- [36] C. Oyarzún, R. Godoy and N.E.C. Verhoest, "Interactions between hydrology and biogeochemical cycles of native vegetated mountain watersheds under different management, southern Chile.", in *Proceedings of the international interdisciplinary conference on predictions for hydrology, ecology, and water resources management: using data and models to benefit society - HydroPredict'2008*, Czech Association of Hydrogeologists. Prague, Czech Republic, 49-52, 2008.
- [37] F. Bärlocher, "Leaf mass loss estimated by litterbag technique", in *Methods to study litter decomposition: a practical guide*, Springer. Berlin, 37-42, 2005.

- [38] J.S. Olson, "Energy Storage and the Balance of Producers and Decomposers in Ecological Systems". *Ecology*, 44(2), 322-331, 1963.
- [39] J.H. Zar, *Biostatistical Analysis*, Prentice Hall, New York, 1999.
- [40] C.A. Pérez, J.J. Armesto, C. Torrealba and M.R. Carmona, "Litterfall dynamics and nitrogen use efficiency in two evergreen temperate rainforests of southern Chile". *Austral Ecology*, 28(6), 591-600, 2003.
- [41] R. Covarrubias, "Notes on the dynamics and decomposition of leaves in a *Nothofagus pumilio* forest". *Environmental Monitoring and Assessment*, 29(3), 253-266, 1994.
- [42] J. Leiva and R. Godoy, "Production and decomposition of litterfall in *Nothofagus* forest in southern Chile", in *Proceedings of the workshop comparison of ecosystems functioning and biogeochemical cycles in temperate forest in southern Chile and Flanders*, Academia Press. Gent, Belgium, 103-106, 2001.
- [43] C.M. Swan and M.A. Palmer, "Leaf Diversity Alters Litter Breakdown in a Piedmont Stream". *Journal of the North American Benthological Society*, 23(1), 15-28, 2004.
- [44] L. Myers, T. Mihuc and T. Woodcock, "The Impacts of Forest Management on Invertebrate Communities Associated with Submerged Leaves in Forested Adirondack Streams". *Journal of Freshwater Ecology*, 22(2), 325-331, 2007.
- [45] N. Kaneko and E. Salamanca, "Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan". *Ecological Research*, 14(2), 131-138, 1999.
- [46] A. Lecerf, G. Risnoveanu, C. Popescu, M.O. Gessner and E. Chauvet, "Decomposition of diverse litter mixtures in streams". *Ecology*, 88(1), 219-227, 2007.
- [47] M.A.S. Graça and M. Zimmer, "Leaf toughness", in *Methods to study litter decomposition. A practical guide*, Springer. Dordrecht, 121-125, 2005.
- [48] R.C. Petersen and K.W. Cummins, "Leaf processing in a woodland stream". *Freshwater Biology*, 4(343-386), 1974.
- [49] J.M. Quinn, G.P. Burrell and S.M. Parkyn, "Influences of leaf toughness and nitrogen content on in-stream processing and nutrient uptake by litter in a Waikato, New Zealand, pasture stream and streamside channels". *New Zealand Journal of Marine and Freshwater Research*, 34(2), 253-271, 2000.
- [50] C.J. LeRoy, T.G. Whitham, S.C. Wooley and J.C. Marks, "Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river". *Journal of the North American Benthological Society*, 26(3), 426-438, 2007.
- [51] S.E. Pérez, C.A. Pérez, M.R. Carmona, J.M. Fariña and J.J. Armesto, "Efectos del fósforo y carbono lábiles en la fijación no simbiótica de N₂ en hojarasca de bosques siempreverdes manejados y no manejados de la Isla de Chiloé, Chile". *Revista Chilena de Historia Natural*, 81(2), 267-278, 2008.
- [52] C.M. Lorion and B.P. Kennedy, "Relationships between deforestation, riparian forest buffers and benthic macroinvertebrates in neotropical headwater streams". *Freshwater Biology*, 54(1), 165-180, 2009.

- [53] C. Robinson, D. Schmid, M. Svoboda and S. Bernasconi, "Functional measures and food webs of high elevation springs in the Swiss alps". *Aquatic Sciences - Research Across Boundaries*, 70(4), 432-445, 2008.
- [54] T.P. Moulton and S.A.P. Magalhães, "Responses of leaf processing to impacts in streams in Atlantic rain Forest, Rio de Janeiro, Brazil - a test of the biodiversity-ecosystem functioning relationship?". *Brazilian Journal of Biology*, 63(1), 87-95, 2003.
- [55] E.F. Benfield, J.R. Webster, J.L. Tank and J.J. Hutchens, "IV. Litter Breakdown and Streams: Long-Term Patterns in Leaf Breakdown in Streams in Response to Watershed Logging". *International Review of Hydrobiology*, 86(4-5), 467-474, 2001.

Effects of management practices on water yield in small headwater catchments at Cordillera de los Andes in southern Chile

Carlos E. Oyarzún¹, Jeroen Staelens², Niko E.C. Verhoest³, Roberto Godoy⁴

¹Instituto de Geociencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.
Email: coyarzun@uach.cl

²Laboratory of Forestry, Ghent University, Geraardsbergse Steenweg 267, B-9090 Gontrode, Belgium. Email: jeroen.staelens@UGent.be

³Laboratory of Hydrology and Water Management, Ghent University, Coupure 653, B-9000 Gent, Belgium. Email: niko.verhoest@UGent.be

⁴Instituto de Botánica, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.
Email: rgodoy@uach.cl

Abstract. In several parts of the world, drinking water is obtained from springs in natural and managed mountainous forests. Since forests regulate quality as well as quantity of water, the effects of forest-management activities on water yield are an important subject of study. The objective of this study was to evaluate the effects of forest management on water yield in managed and unmanaged temperate native rainforests in the Andean range of southern Chile. The study area is located in San Pablo, a forest reserve of 2,184 ha located at the Andean range of southern Chile (39° 35' S, 72° 07' W, 600-925 m a.s.l.). From April 2003 to October 2008, seven experimental small catchments were monitored for rainfall, throughfall, stemflow, soil water infiltration, soil water percolation and runoff. In 2002, one catchment with a secondary deciduous forest was managed, through thinning, causing a reduction in basal area by 35% whereas the other one remained unthinned as control. Both watersheds are adjacent and are located at 600 – 720 m of elevation on deep loam textured volcanic soils (100 - 120 cm). In November 2006, a watershed covered with evergreen old-growth forests was thinned extracting 40% of the total basal area whereas another adjacent catchment remained unthinned as control. Both watersheds are located at 725 – 910 m a.s.l. and have the same aspects. The effects of management of deciduous secondary forests showed that for the period April 2003-March 2007, the mean value of the increase in total annual streamflow was 12.7%, ranging from 10.9% to 14.6%. Thinning of the evergreen old-growth forest increased the streamflow for the period November 2006-October 2008 with 6.1%, ranging from 4.4% to 7.8%, with greater differences during summertime (15.7 to 206%).

1. Introduction

Society's demand for fresh water is continuously growing but this demand might not be satisfied due to the unequal spatial and temporal availability of this resource. Moreover, pollution and an inadequate territorial management in the zones

producing water may result in important decreases of both quality and quantity of fresh water.

The terrestrial water cycle and the impact of climate change have an important influence on water resources and on the potential for flood or drought. Consequently, they are crucial to both agricultural and natural ecosystems. A significant increase in surface runoff is expected in southern Asia whereas a significant decrease is expected in South America [1]. The changes will affect regional environment and socio-economics, through drought and flood, soil degradation, water pollution, food shortages and frequent extreme climate [2].

Studies in central Chile suggest a secular decline in annual precipitation and/or an increase in temperature over the past 200 year [3, 4, 5]. Several precipitation records from the region also indicate a significant long-term decline since mid of the nineteenth century [5]. These apparent long-term precipitation changes are occurring simultaneously with a growing agricultural, industrial, and municipal consumption of water in central Chile and may lead to increased socio-economic sensitivity to climate variability and change [6]. Also, statistically significant reductions in annual precipitation have been detected in other long precipitation record from central Chile, including La Serena, Valparaíso, Concepción, and Valdivia [7]. Projected changes in circulation patterns expressed in the Antarctic Oscillation (AAO) index would decrease summer-fall precipitation and streamflow in southern Chile, with more frequent droughts [8]. In southern Chile, the increase in streamflow in thinned watersheds is also important due to the recent and projected increase in water demand for human consumption, irrigation, tourism, introduced salmon farming and hydropower generation [9].

Under a scenario of global climate change, water supply becomes one of the main ecosystem functions of forests. In their report on the importance of forest protected areas for drinkable water, the World Bank and WWF Alliance for Forest Conservation and Sustainable Use, emphasize the potential role of these areas in helping to maintain water supply to major cities in the world. A large amount of the water available for the world population as drinkable water comes from existing reserves in natural and artificial forests. Forests regulate quality as well as quantity of water, being the base for an integrated management of hydrological resources in forested watersheds. Hence, water supply provides an important argument for forest sustainable management and protection around the world [10].

The hydrological and meteorological role of forests has attracted considerable attention from the public over the last two centuries. However, the first satisfying answers to the question of forest influence on the water cycle came from direct experimentation at the watershed scale [11]. Already from 1900 on the first studies compared watersheds with different forest covers, and first experiments with paired catchments were carried out in the Colorado mountains, at Wagon Wheel Gap, from 1910 to 1926 [11]. These studies mainly focussed on the impact on low flows and

base flows. One of the main concerns about small experimental watersheds is whether the research results obtained can be interpreted and extended to other, larger watersheds [12]. The catchment approach provides a powerful tool to evaluate quantitative changes caused by both natural and anthropogenic alterations [13].

In a review of experimental paired catchments, Brown et al. [14] concluded that reducing forest cover causes an increase in water yield and that coniferous and *Eucalyptus spp.* forests cause larger changes than deciduous hardwoods on water supply. Stednick [15] reviewed results of studies from the United States and looked only at annual water yield changes as a result of timber harvesting. The focus was on the effect of the percentage of area treated to detect changes in streamflow. Different hydrologic areas were defined based on temperature and precipitation regimes and it was concluded that in general, changes in annual water yield from forest cover reductions of less than 20% of the catchment could not be detected by streamflow measurements. The conclusion that at least 20% of a catchment needs to be treated before detectable changes in water yield occur agrees with Bosch and Hewlett [16]. Studies done on deciduous hardwood forests in Central Massachusetts showed that the decrease in total basal area by about 34% resulted in an increase in total streamflow, base flow and groundwater recharge especially in the dormant season [17].

Some studies on the water balance of exotic fast-growing plantations have taken place in South-Central Chile [18,19,20]. These studies are mainly concerned with the interception and transpiration in fast-growing plantations of *Pinus radiata* and *Eucalyptus spp.* Preliminary results in southern Chile [21] have reported that the streamflow was 28% higher in native forest than *Pinus radiata* plantation catchments in a summertime period. However, accurate information on the effect of management of the native forests on water yield is not available. Therefore, the objective of this study was to evaluate the effects of forest management on water yield in managed and unmanaged deciduous and evergreen native rainforests located in the Andean range of southern Chile.

2. Study area and field measurements

In the Andean range of southern Chile (39° 35' S, 72° 07' W, 600 - 925 m a.s.l.) four experimental watersheds with native old-growth and secondary forests were selected: (a) two evergreen pristine old-growth forests, and (b) two deciduous secondary forests. In 2002, a long-term research in hydrology and biogeochemical cycles was started. The experimental design was the watershed-ecosystem approach following the Hubbard Brook Ecosystem Study model [12].

The main tree species of the canopy cover in the watersheds with evergreen old-growth forests are *Nothofagus dombeyi* (Mirb.) Oerst., *Saxegothae conspicua* Lindl., *Laureliopsis philippiana* Looser and *Dasyphyllum diacanthoides* (Less)

Cabr. *N. dombeyi* at San Pablo can have heights up to 55 m. Understorey trees include *Amomyrtus luma*, *Myrceugenia planipes*, *Laureliopsis philippiana* and *Saxegothaea conspicua*. Shrubs that reach heights of over 5 m are composed by *Laureliopsis philippiana*, *Amomyrtus luma*, *Azara lanceolata* Hook f., *Gricelinia scandens* (Ruiz et Pavon) Taub., *Chusquea coleu* Desv. and *Chusquea quila*. The deciduous secondary forests consisted of *Nothofagus obliqua* (Mirb.) Oerst and *Nothofagus alpina* (Poepp. et Endl.) Oerst. The understorey in the unmanaged forests is composed by *Lauriolopsis philippiana*, *Luma apiculata* (DC) Burret, *Nothofagus dombeyi*, *Dasyphyllum diacanthoide*, *Chusquea coleu*, *Gricelinia scandens*, *Raphithamnus spinosus* (A.L. Juss) Mold, and *Aristotelia chilensis* (Mol.) Stuntz. The understorey in the managed forest includes *Aristotelia chilensis*, *Chusquea coleu*, *Rubus constrictus*, *Azara lanceolata* and *Fuchsia magellanica*.

Soils in the study area are Trumaos or Andisols, Typic Dysandrepts originating from volcanic ash of different ages [22,23]. The first stratum of fine ash is 0.5-1.2 m deep and covers an older stratum of pumicitic material with larger diameter sizes. The soils are predominantly well drained with high infiltration rates and are deep (> 100 cm depth). The geological substrate is composed by volcanic rocks.

The climate is rainy temperate and the annual rainfall increases with altitude. The mean annual temperature is 9.0 °C (February mean is 20°C, August mean is 5°C) and the mean annual precipitation is 4000-5000 mm. During the 6-year study period, October 2002-September 2008, the mean annual rainfall was 4868 mm. Rainfall is concentrated during the winter period (May-August, 45%) and decreases strongly in the summer period (January-March, 10%).

Precipitation (P) was recorded with HOBO® tipping bucket rain gauges connected to a data logger and placed in a nearby meadow with no trees within a 40 m radius. Runoff (Q) was measured recorded hourly by data loggers in V-notch weirs (90°) installed in the lower part of each watershed. The interception loss (INT) was calculated following: $INT = P - (Th + St)$, where P = rainfall, Th = throughfall and St = stemflow. Twenty fixed throughfall and ten stemflow collectors were installed in each watershed. Evapotranspiration (EVPT) was estimated according to $EVPT = P - (Q + INT)$.

3. Management practices

From October 2002, one watershed covered with secondary growth forests was thinned, extracting 35% of the total basal area and removing the logs whereas the other one remained unthinned as control (Fig. 1). Both watersheds are adjacent and are located at 600 – 720 m of elevation on deep loam textured volcanic soils (100 – 120 cm) laying over a 90-cm deep pumice layer and a volcanic fossil soil (80 – 100 cm).

In November 2006, one watershed covered with evergreen old-growth forests was thinned, extracting 40% of the total basal area (from 75.9 m² ha⁻¹ to 45.9 m² ha⁻¹) and the other one remained unthinned as a control. Both watersheds are adjacent and are located at 725 – 910 m a.s.l. (Fig. 2).

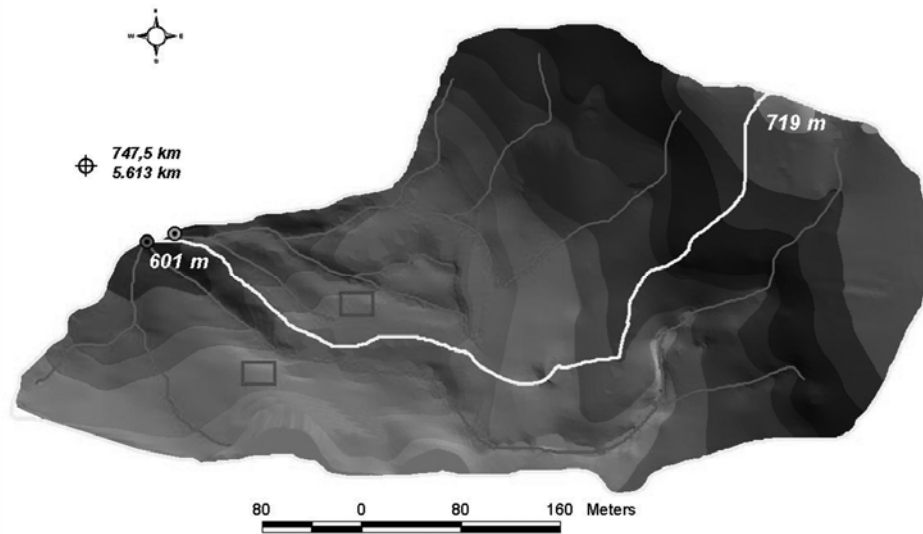


Fig. 1. Location of the managed (lower) and unmanaged (upper) catchments with secondary deciduous forests in San Pablo, Andean range, southern Chile

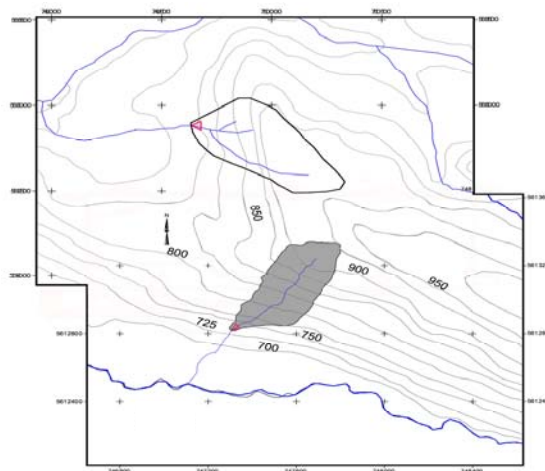


Fig. 2. Location of the managed (grey) and unmanaged (white) catchments with evergreen old-growth forests in San Pablo, Andean range, southern Chile

4. Water yield and forest management

4.1. Deciduous forests

Overall, the thinned watershed yielded higher stream discharge values compared to the control catchment for the four years observation period (April 2003 – March 2007), with greater absolute differences during fall and winter, when 67% of the precipitation is concentrated (Fig. 3). In the managed watershed with deciduous *Nothofagus alpina* secondary forests, water yield was increased from 2642 to 2975 mm yr⁻¹ compared to a control unthinned watershed. The mean value of the increase in total annual streamflow was 12.7%, ranging from 10.9% to 14.6%.

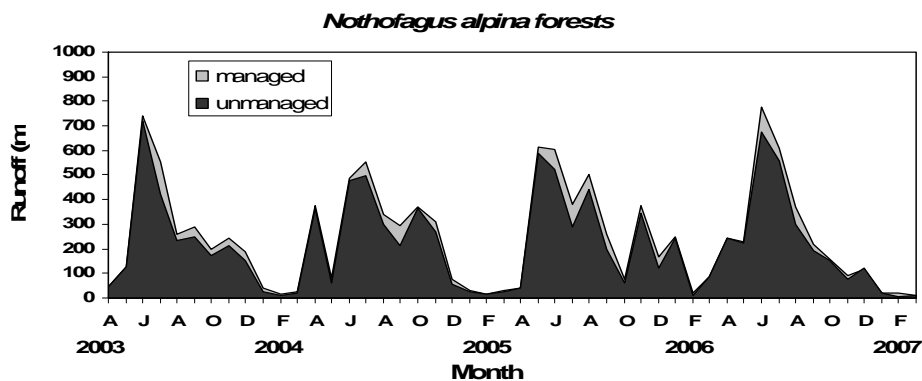


Fig. 3. Monthly streamflow in the thinned and control watersheds with *Nothofagus alpina* forests during four hydrologic years (April 2003 – March 2007)

4.2. Evergreen forests

For the pretreatment period (October 2005-September 2006) the runoff in the control watershed was higher than in the managed watershed (4512 mm yr⁻¹ vs. 4008 mm yr⁻¹). The increase in streamflow in the managed watershed was 4.4% during the post treatment period November 2006-October 2007 (managed = 3105 mm yr⁻¹, control = 2975 mm yr⁻¹) and 7.8% during the period November 2007-October 2008 (managed = 3648 mm yr⁻¹, control = 3384 mm yr⁻¹) (Fig. 4). Larger differences were observed during summertime (15.7% in the first year and 206% in the second year) (Fig. 5).

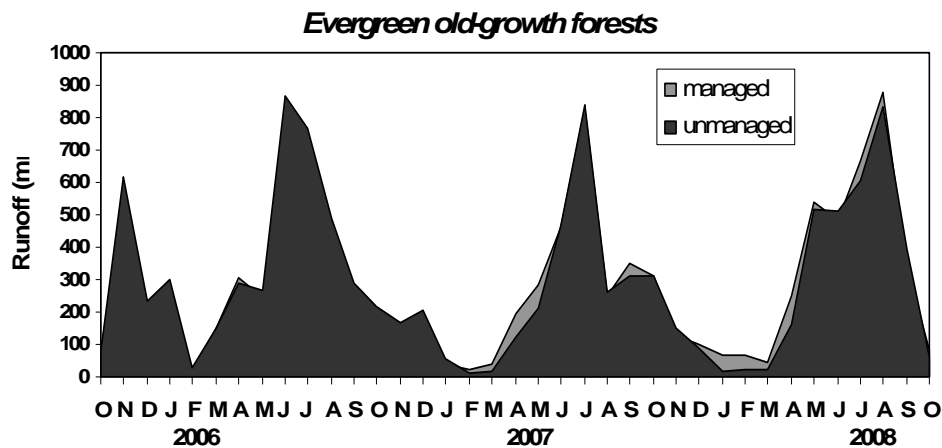


Fig. 4. Monthly streamflow in the thinned and control watersheds with evergreen old-growth forests (October 2005 to September 2008)

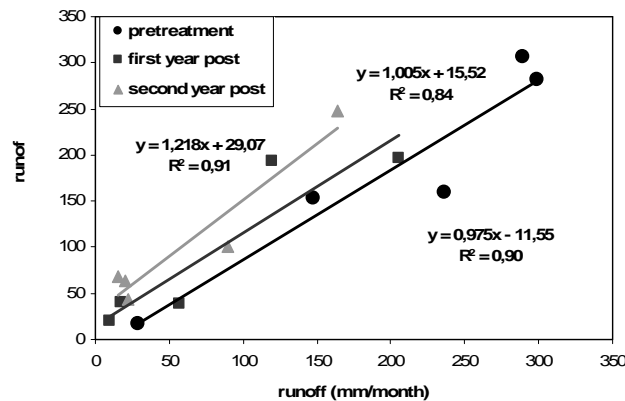


Fig. 5. Relationship between streamflow in the control and thinned watersheds for the pre- and post treatment periods during summertime (January to March)

5. Conclusion

In the managed watershed with deciduous *Nothofagus* secondary forests, during the period April 2003-March 2007, an average increase in total annual streamflow of 12.7% was observed, ranging from 10.9% to 14.6%. The differences in the streamflow between managed and unmanaged forests probably resulted from an increase in throughfall (82.8 %) and a decrease in interception loss (15.4 %) in the managed watershed, compared to the unmanaged watershed (throughfall = 78.5%, interception loss = 18.1%).

Thinning of the evergreen old-growth forest resulted in an average increase of streamflow for the period November 2006-October 2008 of 6.1%, ranging from 4.4% to 7.8%, with larger differences during summertime (15.7% to 206%).

Results of this study provide the first information on the effects of deciduous and evergreen old-growth forest treatment on water yield in central-southern Chile. The

study shows that forest treatment activities by thinning the forest stand with 35% to 40% of the total basal area lead to a significant increase in water yield.

Acknowledgements

This research was supported by the Bilateral Project Chile-Flanders, the Fondecyt Project 1090345 and DIDUACH S-2008-15. We thanks to Prof. Dr. Oswald Van Cleemput for assistance in the revision of the manuscript.

References

- [1] F. Tao, M. Yokozawa, Y. Hayashi, and E. Lin, "Terrestrial water cycle and the impact of climate change", *Ambio*, 32, 295-301, 2003.
- [2] Th. R. Karl, and K. E. Trenberth, "Modern global climate change", *Science*, 302, 1719-1723, 2003.
- [3] R. Villalba, "Tree-ring and glacial evidence for the medieval warm epoch and the Little Ice Age in Southern South America", *Climatic Change*, 26, 183-197, 1994.
- [4] A. Rivera, G. Casassa, C. Acuña, and H. Lange, "Recent glacier variations in Chile", *Revista Investigación Geográfica*, 34, 29-60, 2000.
- [5] B. H. Luckman, and R. Villalba, "Assessing the synchronicity of glacier fluctuations in the western Cordillera of the Americas during the last millennium", in *Interhemispheric Climate Linkages*. Academic Press, 119-140, 2001.
- [6] C. Le Quesne, D. W. Stahle, M. K. Cleaveland, M. D. Therrell, J. C. Aravena, and J. Barichivich, "Ancient *Austrocedrus* tree-ring chronologies used to reconstruct Central Chile precipitation variability from A.D. 1200 to 2000", *Journal of Climate*, 19, 5731-5744, 2006.
- [7] J. Quintana, "Factors involved in the interdecadal precipitation variability in Chile", M.S. thesis, Department of Geophysics, Universidad de Chile, 2004.
- [8] A. Lara, R. Villalba, and R. Urrutia, "A 400-year tree-ring record of the Puelo River summer-fall streamflow in the Valdivian rainforest eco-region, Chile", *Climatic Change*, 86, 331-356, 2008.
- [9] A. Lara, P. Donoso, and L. Nahuelhual, "Los servicios ecosistémicos: una oportunidad para el manejo y conservación de los bosques nativos de Chile", in *Proceedings Econothofagus 2008*. Esquel, Chubut, Argentina, 16, 2008.
- [10] N. Dudley, and S. Stolton, "Running pure: the importance of forest protected areas to drinking water", World Bank in Alliance with World Wildlife Fund for forest conservation and sustainable use. United Kingdom, 2003.
- [11] V. Andreassian, "Waters and forests: from historical controversy to scientific debate", *Journal of Hydrology*, 291, 1-27, 2004.
- [12] G. E. Likens, and F. H. Bormann, "Biogeochemistry of a forested ecosystem", Springer-Verlag. New York. 1995.
- [13] G. E. Likens, "Biogeochemistry, the watershed approach: some uses and limitations", *Marine and Freshwater Research*, 52, 5-12, 2001.

- [14] A. E. Brown, L. Zhang, T. A. McMahon, A. W. Western, and R. A. Vertessy, "A review of paired catchments studies for determining changes in water yield resulting from alterations in vegetation", *Journal of Hydrology*, 310, 28-61, 2005.
- [15] J. D. Stednick, "Monitoring the effects of timber harvest on annual water yield", *Journal of Hydrology*, 176 (1/4), 79–95, 1996.
- [16] J. M. Bosch, and J. D. Hewlett, "A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration", *Journal of Hydrology*, 55 (1/4), 3–23, 1982.
- [17] G.C. Bent, "Effects of forest-management activities on runoff components and ground-water recharge to Quabbin Reservoir, central Massachusetts", *Forest Ecology and Management*, 143, 115-129, 2001.
- [18] C. E. Oyarzún, and A. Huber, "Water balance in young plantations of *Eucalyptus globulus* and *Pinus radiata* in southern Chile", *Terra*, 17, 35-44, 1999.
- [19] A. Huber, and A. Iroumé, "Variability of annual rainfall partitioning for different sites and forest cover in Chile", *Journal of Hydrology*, 248, 78-92, 2001.
- [20] A. Iroumé, A. Huber, and K. Schulz, "Summer flows in experimental catchments with different forest covers, Chile", *Journal of Hydrology*, 300, 300-313, 2005.
- [21] L. Otero, A. Contreras, and L. Barrales, "Efectos ambientales del reemplazo de bosque nativo por plantaciones (Estudio en cuatro microcuencas en la provincia de Valdivia)", *Ciencia e Investigación Forestal*, 8, 252-276, 1994.
- [22] J. Tosso, "Suelos volcánicos de Chile", Instituto de Investigaciones Agropecuarias (INIA). Santiago, Chile. 1985.
- [23] T. T. Veblen, "Forest development in tree-fall gaps in the temperate rain forests of Chile", *National Geographic Research*, 1, 162-185, 1985.

Changes in abundances of parasitoids (Hymenoptera) and others arthropods (Araneae) in managed and unmanaged native rainforests

Yuri Ugarte-Lavados^{1,2,3}, Paul Dassori A.³

¹Programa Doctorado en Ciencias mención Sistemática y Ecología,
Email: yuri.ugarte@postgrado.uach.cl

²Servicio Agrícola y Ganadero, Protección Agrícola, Valdivia, Chile.

³Instituto de Geociencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.

Abstract. The effects of forest-management activities on biodiversity (ecological indicators) and the integrated all effects in one essential element, the flux of water were studied. An important subject of study is the integrated terrestrial key species on biodiversity and flux of water run-off to the watersheds. The native temperate rainforests of southern Chile represent an important reserve of temperate forests and fresh water of the world, and support fundamental ecosystem services such as soil protection, biodiversity conservation, climate regulation, and water quantity and quality control. The watersheds of the rainforest have dominant woody species providing much of the habitat, structure, and resource base for the associated biota in woodland systems. Stress agents that impact long-lived woody species will have cascading effects on the associated communities. Parasitoids wasps (certain taxa of parasitic Hymenoptera) are species-rich and likely to be sensitive indicators of environmental changes. Another ecological indicator of sustainable forest management are spiders (Araneae). Both bio-indicators are species suitable as ecological indicators as their biology is sensitive to disturbance effects of management on the processes or functioning of the ecosystem. We considered a priori hypothesis that there is no significant relationship between the disturbance and measured qualities of the indicators in other areas or at different places. The study area is in San Pablo de Tregua, a forest reserve of 2,184 ha located at the Andes Range of southern Chile. On the other hand, we used the *MapWindow* GIS for delineation and verification of limits or boundaries of each watersheds which was instrumentalized.

1. Introduction

At present our world is in an era of unprecedented ecological changes. These changes are produced by converting natural landscapes for human use. Human activities have been and are continuing to change the environment on local and global scales [1]. The expansion of human population and their increasing consumption rate and access to technology have led to two general environmental concerns [2]: (i) the increasing human impact on the earth's environment and ecosystems through changes in the carbon pools of the biosphere, element cycling, and climate, and (ii) changes in the earth's biota and communities. Many of these

alterations are leading to dramatic changes in the biotic structure and composition of ecological communities, either from the loss of species or from the introduction of exotic species [1].

Global extinction of a species is clearly an important conservation concern. Local species extinction or even large changes in abundances, as seen with many attempts to reintroduce species or eradicate invasive exotics, have a high potential to affect ecosystem properties [3]. These problems affect both managed and unmanaged ecosystems.

The relationship between biodiversity and ecosystem functioning has emerged as a central functioning issue in ecological and environmental sciences [2,4]. The changes in biodiversity alter ecosystem processes and change the resilience of ecosystems to environmental changes [5,6]. This has profound consequences for natural services that humans derive from ecosystems. Many factors influence the magnitude and stability of ecosystem properties, including climate, geography, and soil or sediment type. These abiotic controls interact with functional traits of organisms to control ecosystem properties [1,8]. Feedbacks between human activities, global changes, and biotic and abiotic controls on ecosystems properties, are now sufficiently widespread that their ecological effects have reached global proportions [1,6,7]. The hypothesis that greater ecological diversity leads to greater stability has been a point of interest and debate for half a century [9].

The last half-century of ecosystem ecology research has yielded large amounts of information about how traits on organisms influence ecosystem properties in both terrestrial and aquatic ecosystems, and about trade-off and linkages of these traits to individual organisms [1]. Anthropogenic environmental alterations and human assisted dispersal of exotic species have sparked widespread changes in the global distribution of biota. The resulting modifications have predominantly been in two directions: (i) range expansions of cosmopolitan, non-native species; and (ii) range contractions of regional and endemic native species. This replacement of specific native forms by generalist non-natives in space and time has mixed the taxonomic composition of once disparate biota, an occurrence termed ‘biotic homogenization’ [10].

Biotic homogenization, the gradual replacement of native biotas by locally expanding non-natives, is a global process that diminishes floral and faunal distinctions among regions. Although patterns of homogenization have been well studied, their specific ecological and evolutionary consequences remain unexplored. We argue that our current perspective on biotic homogenization should be expanded beyond a simple recognition of species diversity loss, towards a synthesis of higher order effects. We understand exist three distinct forms of homogenization, whether referring to genetic, taxonomic or functional homogenization, is defined as an increase in the spatial similarity of a particular biological variable over time, and is

usually evaluated by comparing the average pair wise similarity of the variable calculated at two discrete times [10].

An emerging line of inquiry in this research area addresses how species invasions and extinctions increase taxonomic similarity of biotas among sites over time (i.e. decrease β diversity). This process, coined biotic homogenization (BH) [*sensu* 11], describes the gradual replacement of regionally distinct communities by cosmopolitan communities, and is seen to have important ecological and evolutionary consequences [12].

The occurrence and relative abundance of functional traits contributed by constituent species determines the functional diversity of a biological community. They present a conceptual framework where each functional trait is represented by a single axis, and the collection of functional traits contributed by all species of the community defines the n-dimensional hyper volume in functional space occupied by the community. For each single functional trait, species occupy some tolerance range along the environmental axis defined relative to that trait. The cumulative distribution of the trait states of all species represents the aggregate environmental tolerance for the community; therefore, an alteration of species composition (e.g. by invasion or extinction) can modify the overall community tolerance to the environmental condition. The replacement of species with unique trait states (e.g. via the extirpation of rare species) by species with similar trait states (e.g. via the introduction of generalist species) during the homogenization process will truncate the tails of the trait distribution and compress the overall trait range for the community. Consequently, historical differences in the trait distribution among the three communities might be lost, causing them to become homogenized in functional space (i.e. current trait distributions converge toward some common central tendency) [10].

The conceptual framework is extended to a suite of species traits represented in multi-dimensional functional space. The replacement of native species with unique trait states by introduced species with common trait states results in reduced breadth (i.e. trait variation) of the current or homogenized communities in functional space compared to the historical communities. Furthermore, the locations of the communities in functional space are shifted toward a common central tendency, an indication of functional homogenization. Note that, because the ‘winners’ in biotic homogenization are often generalist species [11], the introduction of non-native species will result in reduced within community functional diversity. However, if specialist non-native species are introduced (i.e. species with trait combinations that do not exist in the recipient communities), the within-community functional diversity is expected to increase; however, greater between-community trait similarity is still expected to occur because the same species (and therefore traits) are introduced to the communities [10].

Ecosystem functioning is also a broad term that encompasses a variety of phenomena, including ecosystem properties, ecosystem goods, and ecosystem

services [1]. The concept of ecosystem function distinguishes three classes: stocks of energy and materials (e.g. biomass), fluxes of energy or material processing (e.g. productivity, decomposition), and the stability of rates or stocks over time. Stability of ecosystem processes has been measured as resistance to or resilience from perturbations, predictability, and the inverse of temporal variability [5,6,13]. Many ecosystem functions measured to date fall comfortably into one of these classes, although virtually any aggregate property of an ecosystem could be considered an ecosystem function, such as invasion resistance, the community-wide prevalence of diseases, or efficiency of pollination or seed dispersal [13]. Ecosystem services are those properties of ecosystems that either directly or indirectly benefit human endeavours, such as maintaining hydrologic cycles, regulating climate, cleansing air and water, maintaining atmospheric composition, pollination, soil genesis, and storing and cycling of nutrients [1]. Water is an essential element that provides the ecosystem goods and services.

Water is essential for life on our “blue planet” but just 2.5% of all the Earth’s water comprises freshwater. Of this precious freshwater resource, 0.3% is estimated to be surface water, held in rivers and streams (2%) wetlands (11%) and lakes (87%). Water-dependent habitats are extremely diverse, located from the poles to the equator and from low to high altitude. They comprise dynamic systems that vary in scale from individual plants to large complex vegetation communities, from the smallest headwater stream to the largest lowland river, complex floodplains, a myriad of wetland types, and lentic ecosystems ranging from ponds to vast lakes [14].

A large amount of the water available for the world population as drinking water comes from natural and managed mountainous forests [15]. Dominant woody species provide much of the habitat, structure, and resource base for the associated biota in woodland system, stress agents that impact long-lived woody species will have cascading effects on the associated communities [16].

Arthropods are important components of ecosystems occupying vital positions in food webs, dynamics of populations, and communities. They play various roles in ecosystems acting as herbivores, predators, decomposers, parasites, pollinators, and seed dispersers. Arthropods possess several characteristics that make them suitable for environmental monitoring: high diversity, small body size, high reproductive capacity, acute sensitivity to environmental changes, and ease of sampling. Thus, arthropods are often used as biological indicators of ecosystem integrity [17].

Biological indicators give insight into the status and fluctuations of biological systems. Biological indicators can provide valuable information for prioritizing conservation areas and can be used to advocate better ecosystem management plans. Compared with vertebrates and birds, arthropods have more explicit spatial and temporal scales, highly distinct patch sizes and geographic distributions, more complex seasonal patterns and successional phases, path dynamics with quick turnover, and larger population size. In addition to their inherent characteristics,

there are several practical aspects that make arthropods good indicators of ecosystem integrity, and can be sampled quickly. The use of morphospecies is less time-consuming and often sufficient for environmental monitoring purposes, if the appropriate target group of arthropods is selected. Thus, arthropods could be used reliably to infer ecosystem function and habitat condition [17].

Insects constitute a substantial proportion of terrestrial species richness and biomass, and play a significant role in ecosystem functioning. This realisation has led to extensive discussion and evaluation of the use of terrestrial insects as bio indicators, and the concept has been applied to a variety of taxa, habitats and environmental scenarios. Indicator taxa are used far more frequently to demonstrate the effects of environmental change (such as habitat alteration, or fragmentation and climate change) on biotic systems, rather than functioning merely as gauges of changes in environmental state [18].

2. Watersheds Management

Life on earth depends on sustainable clean water supplies and systematic watershed management is critical to protection of water resources [19]. The hydrological and meteorological role of forests has attracted considerable attention from the public over the last two centuries. Before the French revolution of 1789, some naturalists had already started to express more or less romantic views on the possible influence of forests on climate and water flow. As we have seen, the debate on Water and Forests remained for a long time confined to a romantic and historical argument. The only way out of this dead end was through measurements [20], but more species are needed to insure a stable supply of ecosystem goods and services as spatial and temporal variability increases, which typically occurs as longer time periods and larger areas are considered [1].

In intensively managed systems, management choices influence the diversity of associated species as well as those species targeted for harvest, both within the harvesting area and in the surrounding landscape. Changes in composition and diversity of associated species have potential consequences for forest or agricultural production via supporting ecosystem services (e.g., generation of soil fertility, pest control, pollination), as well as for additional services (e.g., provision of wildlife habitat). Biodiversity clearly has strong effects on ecosystem properties and the goods and services derived from them [1]. Forest harvesting, particularly clear cutting, affects various hydrogeomorphological processes in forest terrain, including enhancement of surface erosion changes in hillslope or catchment hydrology and increases in landslides and debris flows. Just after initiation, landslides and debris flows attributable to the effects of timber harvesting exert significant destructive forces and supply large volumes of sediment to streams, thus increasing catchment sediment changing channel structure and stream ecosystems and threatening property and human habitation downstream [21].

Ecohydrology is an interdisciplinary science focussed on the influence of hydrological processes on biological communities and the feedbacks from biological communities to the water cycle. Progress in understanding these linkages between hydrology and ecology are often limited by lack of long-term, empirical ecohydrological data spanning more than a decade and covering a variety of ecosystems. To address the gradual trends and extreme events that characterize ecohydrological feedbacks, adequate timescales for analysis are especially crucial [20].

The invention of the paired-watershed design consider that the first satisfying answers to the question of forest influence on the water cycle came from direct experimentation at the watershed scale. Clearly, only the paired-watershed design was able to identify the respective roles of the forest cover, “internal” watershed behaviour and climate variability [20].

Watersheds are characterized by meteorological, surface water and groundwater, and physical and biological factors functioning within the context of natural and human disturbance regimes. The quantity, quality, and timing of stream flow within a watershed are influenced by these factors. In order to improve the efficiency of limited conservation resources, the identification of critical areas and human activities that influence water resources is the primary objective of watershed analysis. Biophysical factors (soil, slope, land cover/use, rivers, etc.) and human impacts (road and timber harvest) should be considered systematically in forested watershed management [19].

The principle of the paired-watershed design is based on selecting two watersheds (Fig. 1) as similar as possible (in particular, in terms of size, morphology, geology, climatic forcing and land use). A high degree of similarity leads us to believe that both watersheds will react similarly to climatic inputs. Therefore, we need to monitor both watersheds jointly during a given time period, to understand their differences. Ideally, this preliminary calibration period should vary enough to characterize, as completely as possible, the hydrology of both basins (indeed, they may behave very similarly in average years, and differ more during dry years) [20].

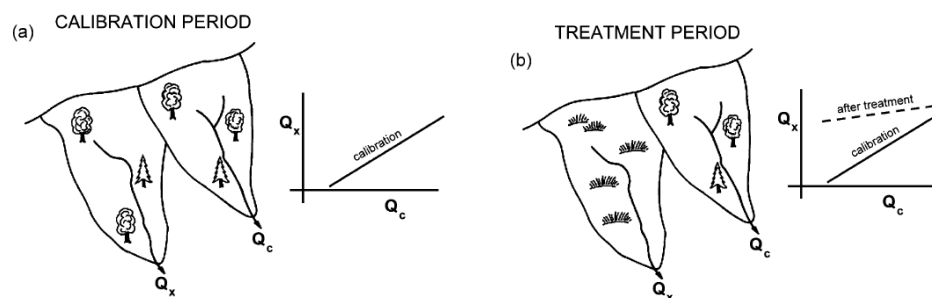


Fig. 1. Sketch of a paired-watershed experiment.

When discussing effects of biodiversity on ecosystem function it is important to be specific about which components of biodiversity are affecting which components of

functioning. Measures of process rates and pool sizes include both levels (e.g. average rates or sizes) and variation (amount of fluctuation). Variation in ecosystem properties can result from fluctuation in the environment from year to year, directional changes in conditions, abiotic disturbance, or biotic disturbance. Biodiversity can be described in terms of numbers of entities (how many genotypes, species, or ecosystems), the evenness of their distribution, the differences in their functional traits, and their interactions. While biodiversity has often been used as a synonym for species richness (the number of species present), different components of biodiversity (e.g. richness, relative abundance, composition, presence/absence of key species) can have different effects on ecosystems properties [1].

The emergence of integrated watershed management (IWM) in several countries throughout the world reflects a growing recognition of the multiple – often competing – use of water, and the increased awareness of the interrelationships of water systems with other physical and socio-economic systems [19].

There is an urgent need to improve our knowledge about the ecological–hydrological interactions in both natural and disturbed environments to assess the implications of land use change on the hydrological cycle. These interactions and feedbacks can have important consequences for streamflow in humid environments, where connectivity between surface and subsurface hydrology is strong. Native forest trees rehydrate after occasional rain events during the dry season, or shortly after the start of the rainy season. Although an explicit focus on ecohydrological interactions is fairly new, the recent advances in this interdisciplinary field has been built on the longer-term research trends in ecology, hydrology, biogeochemistry and geomorphology, which have focused on the interactions between vegetation and the water cycle as primary controls on ecosystem structure. The result of interactions between biologically mediated cycling of water, energy and biogeochemical species is readily apparent as emergent vegetation patterns in the landscape and biogeochemical fluxes. Unlike physical features of the landscape that affect water cycling, vegetation changes occur within relatively short time frames, often due to human influences and management decisions, and also due to natural seasonal or development changes [22].

The native temperate rainforests of southern Chile represent an important reserve of temperate forests of the world, with a high genetic, phytogeographic and ecological significance [23], covering a total area of 10.5 million ha. [24]. These forests support fundamental ecosystem services such as soil protection, biodiversity conservation, climate regulation, and water quantity and quality control. Under a scenario of global climate change, water quality and water supply becomes one of the main ecosystem functions of forests. Forests regulate quality as well as quantity of water, being the base for an integrated management of hydrological resources in forested watersheds.

It has been proven that mountain forest ecosystems are very efficient in trapping nutrients from clouds and fog, especially in the case of nitrogen and base cations. In cloud or fog dominated coastal and mountain regions, ecosystem hydrology and nutrient dynamics might be closely linked to occult precipitation, and occult precipitation contributes significantly to nutrient dynamics in the native forest located at high altitude in the Cordillera de los Andes of southern Chile. Also, fog and clouds can be important sources of nitrogen in N-limited forest ecosystems in southern Chile [25].

3. Structure of Forest Ecological Communities

The oldest and one of the most fundamental patterns concerning life on earth is the increase in biological diversity from polar to equatorial regions. Latitudinal gradients of biodiversity are ultimately dependent on the historical, geographic, biotic, abiotic, and stochastic forces, affecting the geometry, internal structure, and location of species ranges in ecological or evolutionary time. Indeed, latitude is a surrogate for a number of primary environmental gradients (e.g. temperature, isolation, seasonality) that interact and are correlated to each other, making direct tests of hypotheses difficult and controvertible [26].

All terrestrial communities based on living plants are composed of at least three interacting trophic levels: plants, herbivores, and natural enemies of herbivores (e.g. predators, parasitoids, parasites). Recognition of the diverse and important ecosystem services provided by insects and increased awareness of the large proportional contribution of insects to fauna biodiversity have fostered appreciation for the roles insects play in maintaining forest ecosystem health [27].

Food webs are collections of species that are linked by trophic interactions, and are an important unit of biodiversity. They are also inherently spatial entities, made so by species using dispersal as a means of both procuring key resources and avoiding natural enemies. Food web complexity is based on two properties. The first is local niche partitioning, the ability of species to coexist within a community by partitioning resources and/or natural enemies in the absence of any differences between species in when or where they exploit resources or respond to natural enemies (i.e. no spatial or temporal niche partitioning). When two or more species are limited by a single niche axis (e.g. a single limiting resource or natural enemy), local niche partitioning is not possible. In contrast, when two or more species are limited by multiple niche axes (e.g. multiple resources and/or natural enemies), local niche partitioning is possible [27].

Another view, human activities in forests can drastically alter insect communities by directly influencing food resources for phytophagous and detritivorous species, and thereby indirectly influencing food resources for predaceous and parasitic species. However, much of the research examining relationships between plants and insects in forested ecosystems to date has focused on devising silvicultural practices

to cope with insect pests; while relatively little attention has been given to increasing understanding of the underlying mechanisms controlling abundance and biomass of entire insect communities in seemingly healthy forests [28].

This ecological reason argument that all species were not created equal. It is well known that the most abundant species play a mayor role in controlling the rates and directions of many community and ecosystems processes. These dominant species (foundation species) are often crucial for the maintenance of their communities, because they typically provide the major energy flow and the three-dimensional structure that supports other organisms. In many ecosystems, a single foundation species controls population and community dynamics and modulates ecosystem processes. The loss of foundation species acutely and chronically impacts fluxes of energy and nutrients, hydrology, food webs, and biodiversity [28]. However, an important factor are human activities, including logging and the introduction of exotic pests and pathogens, often functionally removing foundation tree species from forests [29].

Vegetation characteristics such as species richness, species diversity, structural complexity, biomass, and composition influence patterns of abundance of insects. Despite ample evidence of strong linkages between plants and insect abundance in particular circumstances, unified principles underlying these relationships across ecosystems have not emerged. Analyses that enable evaluation of the relative strength of associations between vegetation characteristics and abundance of insects in a variety of settings would improve understanding of the relative importance of different mechanistic hypotheses, helping settle the debate over which vegetative factors are most influential [30].

High diversity (abundance) of plants can support high diversity (abundance) of herbivores, which can support high diversity (abundance) of predators. On the other hand, changes in plant diversity and abundance generally involve changes in vegetation structure and in abundance of alternative food. These changes may directly affect diversity and abundance of predators and parasitoids [31,32].

Woodland habitats are among the most stable elements of human-dominated landscapes, which now cover a substantial proportion of the Earth's surface. The parasitoids as such, they play an important role in the maintenance of biodiversity [31]. Most research and the theory of spatial dynamics of the food web have been synthesised in [27]. This research pay particular attention to invariant properties, mechanisms operating in competitive and pairwise consumer-resource interactions that also appear in food web modules, and novel properties, mechanisms that emerge from the interplay between food web dynamics and spatial processes [27].

Metacommunity dynamics have been investigated in both the intraguild predation (IGP) and predation modules. Spatial coupling has been investigated in the omnivory module and in a modified predation module (consumer-resource webs in

different localities are linked by predator foraging). Metacommunity dynamics of the IGP and predation modules differ from those of exploitative and apparent competition. This is because of the potential interplay between local and spatial coexistence mechanisms. Local consumer coexistence can occur via an interspecific trade-off if the inferior resource competitor is less susceptible to a common predator (e.g. keystone predation) or preys on or parasitoids the superior competitor. Such a trade-off is typically considered to arise from life history differences. It can also arise via limited movement of individuals within spatially structured local communities. For instance, two consumer species that differ in their reproductive rates but have similar levels of predator susceptibility (i.e., no life history trade-off) can coexist if the consumer with the higher reproductive rate (superior competitor) attains a more clumped spatial distribution and is therefore subject to more predator attacks than is the consumer with a lower reproductive rate (e.g. inferior competitor). Long-term coexistence requires intermediate rates of predator attack, with lower or higher attack rates causing the exclusion of the inferior and superior competitors, respectively. The two types of metacommunity dynamics (extinction-colonization versus emigration-immigration) have quite different effects on food web persistence and diversity [27].

The role of ecological processes, such as bottom-up and top-down forces on herbivore populations, is often considered to be specific to particular ecosystems, the bottom-up effects of plants being more effective in trophic interactions in terrestrial systems. The cascading effects of bottom-up forces can be detected as indirect effects of heterogeneity (i.e. differences in species richness, abundance, productivity and quality) of plants on third trophic levels through herbivorous insects. However, variation in host-plant characteristics may have differential effects on a herbivore and its associated natural enemies [33].

The ecological indicators have the context they refer to 'species that are known to be sensitive to habitat fragmentation, pollution, or other stresses that degrade biodiversity'. These species represent the response of at least a subset of other organisms to such stresses and thus are, as defined here, ecological indicators [18].

Environmental indicators are also descriptive in that they directly indicate changes in the state of the abiotic environment. Both biodiversity and abiotic environmental changes can be measured directly, although indicator species provide a cheaper method of doing so. Ecological indicators differ from biodiversity and environmental indicators in that they indicate functional changes to systems. They demonstrate the effects of environmental change on the biotic systems including species, communities, and ecosystems. Biological indicators of sustainable forest management are ecological indicators in that they must provide information on the effects of forest management on the functioning of the forest ecosystem to be useful. They can be keystone species, dominant species, sensitive species or species that reflect the ecological effects of a disturbance regime. To be most effective some must target anticipated stresses that are known to result from current or

potential forest management approaches. This requirement for a bioindicator of sustainable forest management to have a functional role, rather than a descriptive role, provides a more concrete basis for interpreting the importance of change [34].

The *Hymenoptera* are one of the four mega-diverse orders of holometabolous insects, along with *Coleoptera*, *Diptera*, and *Lepidoptera*, which dominate the faunas of terrestrial areas throughout the world. *Hymenopterans* live in virtually all terrestrial and freshwater habitats and play numerous ecological roles. Many *Hymenoptera* are critical pollinators or seed dispersers of flowering plants; others help keep populations of insects and other arthropods in check through predation or parasitism; and still others feed on plant or fungal tissue directly. It has been suggested that no other order of insects contains so many species beneficial to humans [35].

Parasitic wasps are known to play an important role in ecosystems through complex interactions within communities of host species, including an ability to suppress populations of herbivorous insects [36,37]. Habitat fragmentation has not only been found to affect insect abundance and diversity, but may potentially alter interactions between insects and other organisms [38]. Parasitic *Hymenoptera*, the major group of insects having the parasitoid life style, are extremely species rich and of wide significance in terrestrial ecosystems. Evidence was also advanced that many groups of Hymenoptera are particularly sensitive to environmental disturbance, which makes their populations especially prone to extinction – the familiar correlate of specialisation. Parasitic *Hymenoptera* often depend on unreliable resources because they belong to a high trophic level. Most species within the group are highly specialised and, in general, more specialised species are more sensitive to changes in the trophic level [39].

Additionally, the haplodiploid sex determination in the *Hymenoptera*, whereby males arise from unfertilized eggs and transmit only the genome of the mother, can reduce genetic variation and fitness, and impose a high minimum viable population size. These characteristics may result in low and variable population sizes for parasitic wasps and such populations are prone to extinction and are sensitive to habitat fragmentation. Despite their potential use as indicators of habitat change in conservation-oriented management, parasitic wasps have been largely neglected to date, probably due to our poor taxonomic and ecological knowledge of them [39].

The habitat requirements of parasitic *Hymenoptera*, particularly the effects of habitat disturbance, have rarely been investigated, and the vast majority of studies have examined natural enemies associated with economically important insect pest, usually in agroecosystems. Studies examining the effects of forest management on insect biodiversity focus mainly on taxa belonging to lower trophic levels, e.g. saproxylic beetles, while parasitoids, including saproxylic parasitoids (i.e. those associated with saproxylic insects), have been investigated only rarely. Some authors found that habitat fragmentation affects parasitoids more than their hosts,

suggesting that parasitoids might be more than their sensitiveness to habitat change [40].

The parasitoids must locate and evaluate the host, evade or overcome the host immune response, and adapt to or regulate a constantly changing host environment to satisfy the metabolic, nutritional, and ecological needs of the immature parasitoids. Parasitoids from diverse origins have evolved a variety of strategies to exploit their host, and understanding the underlying mechanisms, the ecological consequences of host-parasitoid relationships, and the evolutionary processes has interested for scientists. Immature parasitoids are exploitative organisms that live in continuous, intimate association with their host, and important advances have been achieved that characterize patterns of parasitoid preimaginal development, notably optimal resource allocations with the host, and adaptations that promote parasitoids virulence [40].

Parasitoids (mainly wasps) develop to maturity by feeding on or in the bodies of other arthropods, eventually killing them, performing essential ecosystem services in the regulation of other insect populations. This is a valuable resource for use in biological control. It makes them a risk for population decline and extinction. They should serve as a sensitive indicator of environmental threats. However, almost no conservation or monitoring work specifically involves parasitic Hymenoptera outside an agricultural context, despite increasing accessibility of the group, thanks to recent introductory texts and taxonomic literature [41].

The impact of anthropogenic disturbance or forest fragmentation is likely even more important in higher trophic levels than levels to adapt to these changes. Parasitoids and hyperparasitoids are thus organisms for which severe impacts are expected, as they represent the third and fourth trophic levels. Parasitoids develop in (endoparasitoids) or on (ectoparasitoids) hosts, on which they are dependent to complete their development. This level of dependence, however, is different in koinobiont parasitoids, which kill their hosts only when their development is completed, compared with idiobiont parasitoids, which kill their hosts at oviposition or shortly after. Koinobiont parasitoids thus have the additional constraint that their hosts must remain alive throughout their development [41].

In native unmanaged forest ecosystems, the tritrophic interactions between plants, herbivorous insects, and their natural enemies (predators, parasitoids, and pathogens) result from a long coevolutionary process specific to a particular environment and relatively stable climatic conditions. These tritrophic interactions are affected by climatic changes in diverse ways. Temperature changes may influence the biology of each component species of a system differently, provoking a destabilization in their population dynamics that may lead to the extinction of part of the system. Successful parasitism depends both on the capacity of the adult parasitoid to locate and evaluate its host and on the capacity of the larva to evade or overcome the host immune response and adapt to or regulate a constantly changing

host environment, characteristics that could be disrupted by changes in environmental conditions. Understanding the consequences of climate variability on the third trophic level is of fundamental and applied importance, especially when predicting pest outbreaks or by using parasitoids in biological control programs [41].

The interior of old-growth unmanaged forests conserve a low temperature, but the managed forests have a variable temperature. For this reason, morphological adaptations have enabled parasitoids to survive extreme temperatures. Colour plays an important role in thermoregulation; clear individuals are reflective whereas dark colours contribute to more efficient heat absorption. Many parasitoid species exhibit a large variability in their colour morphs, representing adaptive responses to winter conditions [41].

Other arthropods, *Araneae*, as bioindicators, provide a clear context for developing explicit indicator objectives. Our motivation is to demonstrate that bioindicators (parasitoids and *Araneae*) can and should be considered in a broader context than as indicators of environmental disturbance, reflecting the response of multiple (unmeasured) species. Specifically we argue that the principal job of indicators is to capture underlying changes in ecosystem functioning and integrity not to indicate disturbance per se or other species. A single bioindicator species or assemblage is expected to be one component of a team of bioindicators to provide a multi-scaled and holistic assessment of sustainability. Conservation of the biodiversity will follow from maintaining ecosystem integrity [34].

Spiders exhibit an immediate response to clearcut logging (although not necessarily selective harvesting). Clearcutting results in a shift in species composition from forest species to open-habitat species, often resulting in higher overall species diversity. The existing forest species may persist for up to 2-years post-logging, with gradual replacement by open habitat species. Open habitat spiders tend to be from the active hunting families (e.g. *Lycosidae*) and forest species from the microweb-building families (e.g. *Linyphiidae*, *Erigonidae*). Therefore, in spiders a gradual change in family composition is observed over time post-logging. As harvested areas regenerate, the vegetation structure develops providing an environment increasingly suitable for microweb-building spider species and requiring a more sheltered microclimate. Eventually forest fauna would be expected to return [34].

We considered a priori hypotheses H_{01} : there is no significant relationship between the disturbance and measured qualities of the indicator in other areas or at different places. H_{02} : the relationship between the disturbance and other taxa is different to the relationship discovered in the previous step.

4. Study site and field measurements

In the Andean range of southern Chile (39° 35' S, 72° 07' W, 600 - 925 m a.s.l.), (Fig. 2) we selected four experimental watersheds with native old-growth and secondary forests: (a) two evergreen pristine old-growth forests and (b) two deciduous unmanaged secondary forests. The project started in 2002 with a long-term research in hydrology and biogeochemical cycles. The experimental design was the watershed-ecosystem approach following the Hubbard Brook Ecosystem Study model [42].

The main tree species of the canopy cover in both the pristine and altered watersheds with evergreen old-growth forests are *Nothofagus dombeyi* (Mirb.) Oerst., *Saxegothaea conspicua* Lindl., *Laureliopsis philippiana* Looser and *Dasyphyllum diacanthoides* (Less) Cabr. The deciduous secondary forests consisted of *Nothofagus obliqua* (Mirb.) Oerst and *Nothofagus alpina* (Poepp. et Endl.) Oerst.

Precipitation (P) was registered with HOBO[®] tipping bucket rain gauges connected to a data logger and placed in a nearby meadow with no trees within a 40-m radius. We recorded a mean precipitation of 3,926 mm yr⁻¹ for the period April 2003-March 2007, with 66% concentrated in autumn and winter and 7% in summer. Runoff (Q) was measured by pressure transducers DIVER and recorded hourly by data loggers in V-notch weirs (90°) installed in the lower part of each watershed.

We used the experimental design and the monitoring of ecological indicators. These ecological indicators were parasitoids wasps (*Hymenoptera*) [38] and spiders (*Araneae*) [34]. Parasitoids wasps are species-rich and likely to be sensitive indicators of environmental change. Malaise traps are widely used for sampling certain taxa of parasitic *Hymenoptera*, but little is known about how they should best be used to monitor the community at an individual site [43].

5. Management Practices

From October 2002, a single watershed covered with secondary growth forests was thinned; extracting 35% of the total basal area and the logs were removed whereas the other one remained unthinned as control. Both watersheds were adjacent and are located at 600 – 650 m of elevation on deep loam textured volcanic soils (100 - 120 cm) laying over a 90 cm deep pumice layer and a volcanic fossil soil (80 – 100 cm).

In November 2006, a watershed covered with evergreen disturbed old-growth forests was thinned; extracting 40% of the total basal area (from 75.9 m² ha⁻¹ to 45.9 m² ha⁻¹) and the other one remained unthinned as control. Both watershed were adjacent and are located at 725 – 910 m a.s.l.

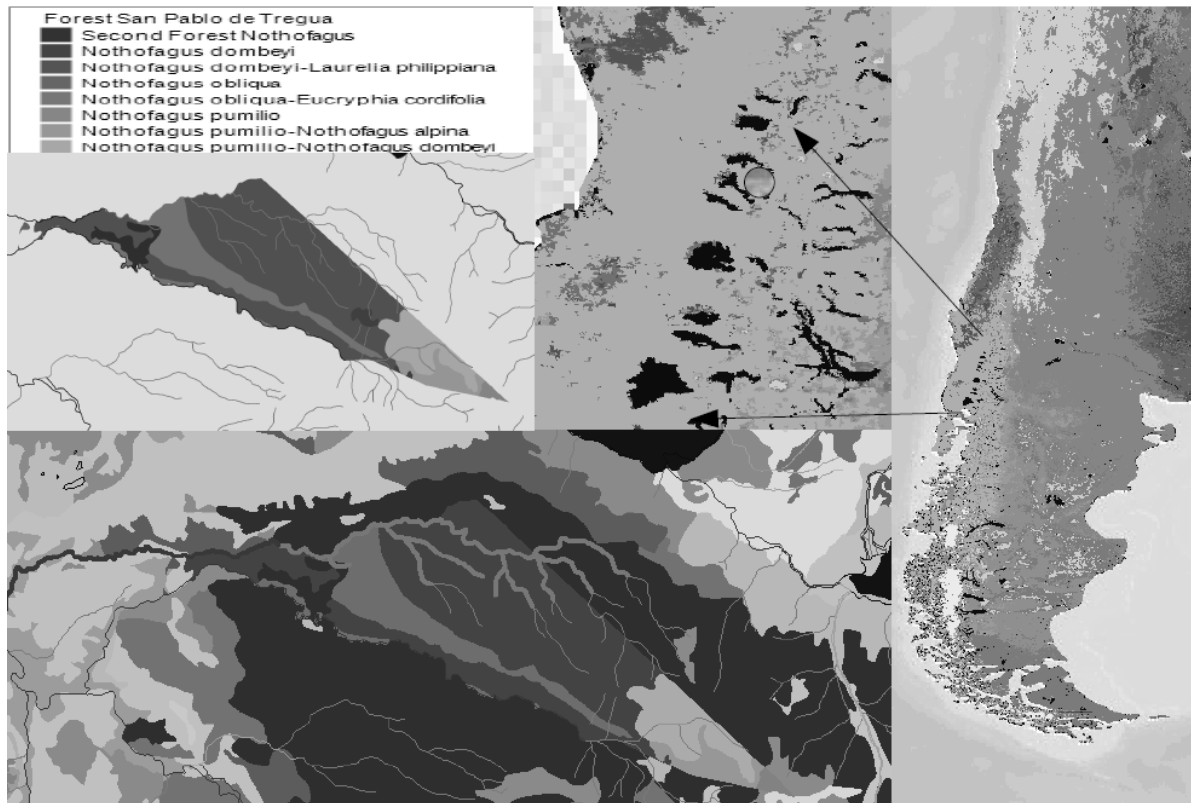


Fig. 2. Overview of the study area “San Pablo de Tregua”(39° 35’ S, 72° 07’ W, 600-925 m a.s.l.) in Andean Range Southern Chile.

6. The watershed model

The purpose of the WaterBase project (<http://www.waterbase.org>) was to advance the practice of Integrated Water Resources Management (IWRM) in developing countries, predictive modelling and decision support for water management in watersheds. At the same time there was increasing availability on the internet for free GIS data, and standard PCs with high processing speeds and storage capacities on relatively cheap and common feasible hardware. The WaterBase project aimed at exploiting this situation, in three phases. In the first, current, phase a free, open source tool for hydrological modelling and scenario exploration is being developed. The tool is intended to be instant anywhere in the world using GIS data from the web, supplemented by more detailed local data if available.

The *MapWindow* GIS and *MWSWAT*, both systems are now free. The *MWSWAT* is an open source interface to Soil & Water Assessment Tool (SWAT), consisting of the GIS system MapWindow and the MapWindow-SWAT interface MWSWAT. Broadly, MWSWAT provides the same functionality as ArcSWAT. MapWindow and MWSWAT is available from the WaterBase website [44]. Simulation programs implementing models of watershed hydrology and river water quality are important

tools for watershed management for both operational and research purposes. In recent years many such simulation programs have been developed such SWAT (Soil and Water Assessment Tool) [45]. Distributed land cover data were derived from HydroSHEDs (high-resolution elevation data from Shuttle Radar Topography Mission – SRTM).

SWAT [45,46] has a substantial reputation as model to quantify the impact of land management practices in large, complex watersheds, and has been used in many developing countries as well as in its home country, the US. Like other modeling tools, it requires a lot of data about terrain, landuse, soil, and climate. There are two essential components needed to set up SWAT models: (a) a GIS system to support the storage and display of the relevant maps, and to perform the terrain analysis needed to delineate watersheds, to identify the stream reaches and the associated micro basins, and (b) a component that can generate all files needed by SWAT, partly from the input maps and analyses, and partly by manual editing.

In fact, MapWindow does have a watershed delineation tool, using the TauDem software [47]. In fact Taudem's use of the *Dinf* approach to slope directions, instead of the normal *D8*, promised better watershed delineation than found in the current ArcSWAT interface. MapWindow is also intended to be extensible through the use of "plug-in" architecture, so it was in fact technically suitable. So, an interface for setting up SWAT was created based on MapWindow, and called MWSWAT. The rest of this paper describes some of the details of MWSWAT and what is additionally needed to be done to provide decision support for IWRM.

7. Data sources

There is a considerable amount of data available on the web, and MWSWAT is designed from the start to take advantage of that issue in mind. In particular it will be delivered along with global data:

1. DEM maps: SRTM project (SRTM, 2004) [48];
2. Land: Global Land Cover Facility; Soil maps [44].

8. Watershed delineation.

Watershed delineation uses a plug-in included in Map-Window. First, the digital elevation (DEM) is chosen, and options to burn in existing streams. After the watershed delineation process is completed, all layers are displayed in the MapWindow view.

9. HRU creation

SWAT uses the Hydrological Response Units (HRUs) as the basis for its modelling. HRUs may be formed per sub-basin (where a sub-basin is the area that drains into a reach of the stream network), or as a division of a sub-basin based on a particular combination of land use, soil, and slope range. The Create HRUs form allows users

to first select the land use and soil maps, together with database tables (lookup tables), which relate the categories used in these maps to SWAT land use and soil categories. Then users can select intermediate slope percentages so as to form bands of slopes. At this point the maps are read. Then the user can choose single HRUs (i.e. one per sub basin) or multiple HRUs. In the second case, the user removes small HRUs, either by selecting a minimum area, or by selecting minimal percentages for land use, soil and slope. Users may optionally also select micro basins at whose exit points reservoirs are situated, may choose to subdivide land uses into others, and may choose to exempt some land uses from the thresholds.

10. SWAT setup and run

The final step is to read the meteorological data, write the SWAT files in the proper format and run the model. The SWAT Setup and Run form allows the user to select weather sources (currently weather stations, plus precipitation and temperature gauges), to choose the period of simulation, or use our time series date base. Users can also choose to make detailed edits to the input files using the SWAT Editor, can run SWAT itself, and can save the output from the latest SWAT run. In brief, this form is the main control of the model itself. It is fully based on the current SWAT development and if required can be modified to keep pace with future changes. Because the entire application is open source, advanced users can even have access to the source code and compile their own DLL for further development. DISPLAYING SWAT OUTPUT once the model produces the output files; the Swat2Dat tool allows the selection of the desired sub-basin to use and produces Ascii files from the SWAT reach output file. This can be directly imported into a spreadsheet for further analysis and plotting. The export tool will be eventually incorporated into the MWSWAT interface. For now, it is an independent program that works also for all the different versions of ArcView SWAT. The current ArcMap version for SWAT was also tested for a basin with calibration data available (our date base). It is worth noticing that both interfaces ultimately run the same and most recent version of the model Swat2005. The results, in the testing basin, are as expected very similar for both platforms with respect to flows.

11. PARASITOIDS (Hymenoptera: *Ichneumonidae*) and ARANEAE

We collected monthly (720 hours), in spring and summer 2006-2007, by use of Malaise traps for monitoring Ecological indicators, parasitoid wasps (*Hymenoptera:Ichneumonidae*). We recently designed our monitoring with the orientations and conclusion [43]. We used statistical analyses of contingency through the Pearson's squared Chi test, χ^2 (see Table 1), calculated by:

$$\chi^2 = \sum \frac{(f_{ij} - e_{ij})^2}{e_{ij}}$$

Our results suggest that the abundances of parasitoids (Hymenoptera: *Ichneumonidae*) differed significantly ($16,1151433 > 5,992(2,0,0.5)$) in the Ecotone zone (more abundance) compared with the old-growth unmanaged forests.

Table 1: Analyses of contingency used to compare the relative abundance of parasitoids (summer 2006-2007).

Forest	Dec-Jan	Jan-Feb	Feb-Mar	Total
Unmanaged	1	0	4	5
χ^2	1,513761468	2,47706422	1,00917431	
Ecotone	32	54	18	104
χ^2	31,48623853	51,5229358	20,9908257	
Total	33	54	22	109

Another collected monthly ecological indicator (Hymenoptera and spiders) was since spring 2007 (November 07) till autumn 2008 (June 08). In this collected accounting, the relative abundance was measured of wasps (*Hymenoptera: Aculeata*) and *Araneae* in old-growth, and second-growth managed and unmanaged forests and the Ecotone zone (with exotic coniferous) (Fig. 3, 4, 5, 6). The not yet considered relative abundance was in the old-growth unmanaged forest between May-Jun 08; the old-growth managed forest (Jan-Feb 08); the Ecotone zone (Jan-Mar 08); and the second-growth managed forest (May-Jun 08).

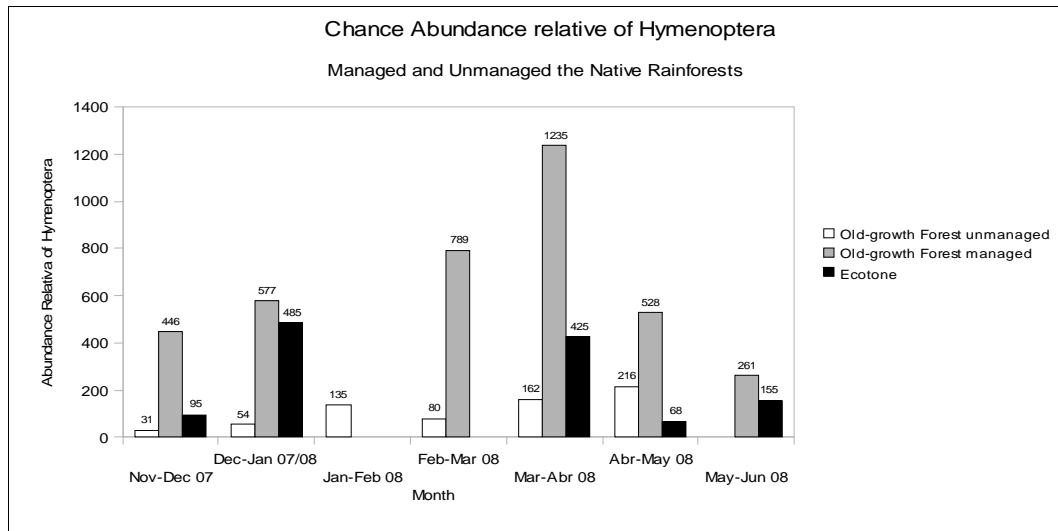


Fig. 3. Relative abundance of *Aculeata* (*Hymenoptera*) in old-growth managed and unmanaged forest (November 2007 – June. 2008)

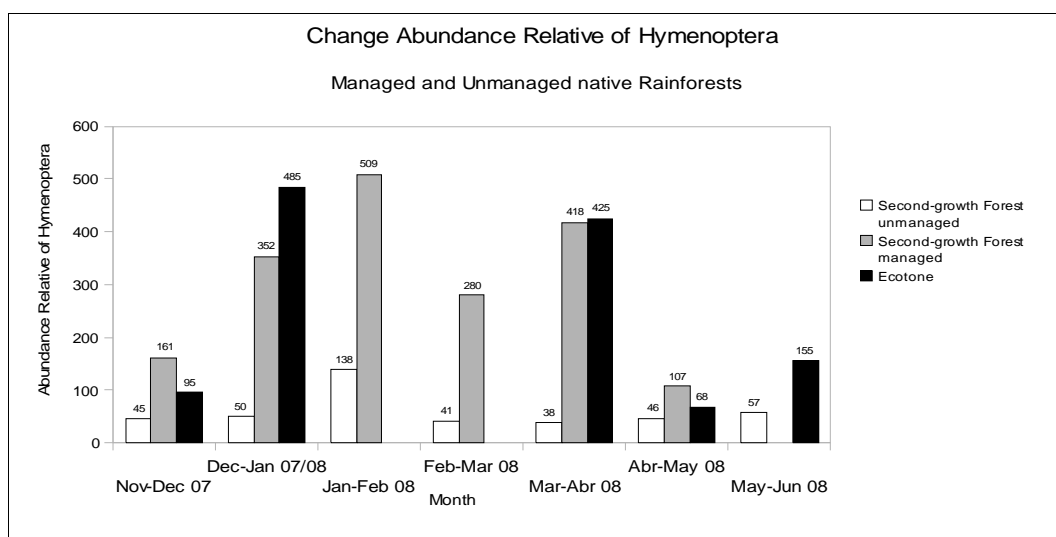


Fig. 4. Relative abundance of *Aculeata* (*Hymenoptera*) in Second-growth managed and unmanaged forest (November 2007 – June 2008)

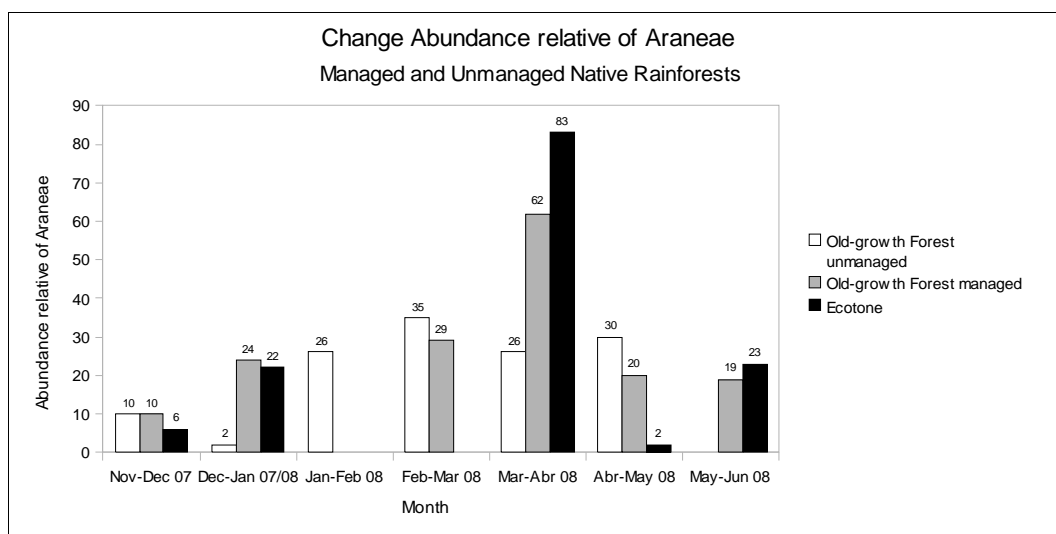


Fig. 5. Relative abundance of *Araneae* in old-growth managed and unmanaged forest (November 2007 – June. 2008)

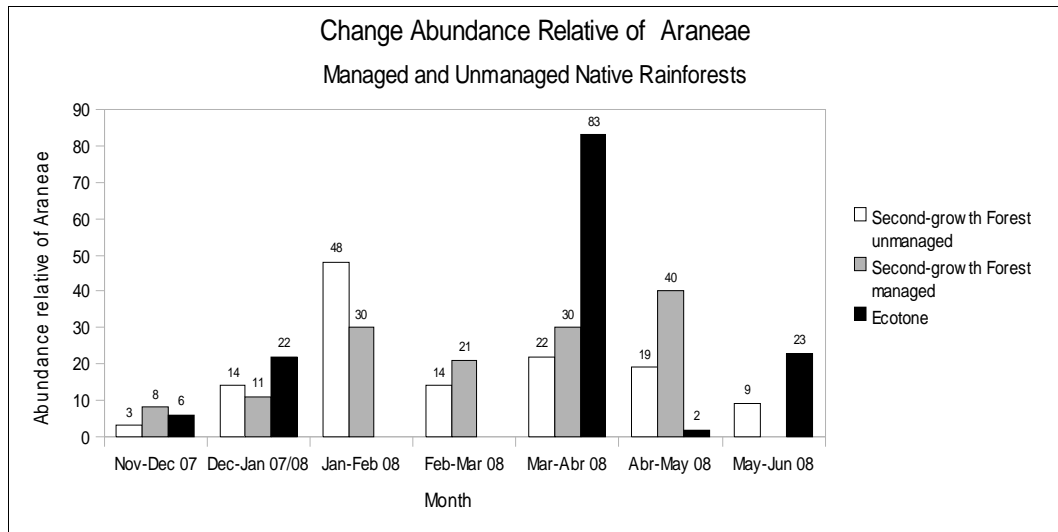


Fig. 6. Relative abundance of *Araneae* in old-growth managed and unmanaged forest (November 2007 – June. 2008)

12. Conclusions

We initially observed the relative abundance of *Aculeata* (*Hymenoptera*), increasing in the old-growth managed forest and the Ecotone zone, compared with the unmanaged old-growth forest (Fig. 3). The same pattern was observed for the second-growth managed forest and the Ecotone zone, compared with the second-growth unmanaged forest (Fig. 4). However, this pattern was not clear for *Araneae* (Fig. 5 and 6). After management, the micro-environments influence insect communities in the understory of forests. For example, canopy gaps provide light to the forest understory and positively affect communities of *Homoptera*, *Diptera* and other insect groups. Additionally, the abundance and species richness of wasps are higher in disturbed forest sites which had more light and cover of understory plants. Adults of all the wasps presumably feed on floral and extra-floral nectar. Vegetative rich environments in the forest understory could provide more food resources, both of prey and nectar, for the wasps. The species richness of understory flowering plants was used to indicate the conditions of local habitats. These conditions of micro-environments include various factors, such as presence of other organisms, soil type and canopy density, which alters light penetration, temperature and moisture. However, vegetation must reflect these biotic and abiotic factors, which act together in setting the stage of an environment, and therefore is simpler to use as indicator [49].

References

- [1] D.U. Hooper, F.S. Chapin, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H. Lawton, D.M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A.J. Symstad, J.

- Vandermeer, and D.A. Wardle, "Effects of biodiversity on ecosystem functioning a consensus of current knowledge" *Ecological Monographs*, 75(1), 3-35, 2005.
- [2] P.M. Vitousek, H. A. Mooney, J. Lubchenco, and J. M. Melillo, "Human Domination of Earth's Ecosystems" *Science*, 277, 494-499, 1997.
- [3] S.A. Zimov, V.I. Chuprynin, A.P. Oreshko, F.S. Chapin, J.F. Reynolds, and M. C. Chapin, "Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene" *American Naturalist* 146, 765-794, 1995.
- [4] M. Loreau, S. Naeem, P. Inchausti, J. Bengtsson, J.P. Grime, A. Hector, D.U. Hooper, M.A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D.A. Wardle, "Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges" *Science*, 294, 804-808, 2001.
- [5] J. Bengtsson, P. Angelstam, T. Elmqvist, U. Emanuelsson, C. Folke, M. Ishe, F. Moberg, and M. Nyström, "Reserves, Resilience and Dynamic Landscapes" *Ambio* 32(6), 389-396, 2003.
- [6] L.H. Gunderson "Ecological Resilience-in Theory and Application" *Annual Review Ecology and Systematics* 31, 425-439, 2000.
- [5] F.S. Chapin, B.H. Walker, R.J. Hobbs, D.U. Hooper, J.H. Lawton, O.E. Sala, and D. Tilman, "Biotic control over the functioning of ecosystems" *Science*, 277, 500-504, 1997.
- [7] F.S. Chapin, E.S. Zavaleta, V.T. Eviner, R.L. Naylor, P.M. Vitousek, H.L. Reynolds, D.U. Hooper, S. Lavorel, O.E. Sala, S.E. Hobbie, M.C. Mack, and S. Díaz, "Consequences of changing biodiversity" *Nature*, 405, 234-242, 2000.
- [8] J.A. Foley, R. DeFries, G.P. Asner, C. Bradford, G. Bonan, S.R. Carpenter, F.S. Chapin, M.T. Coe, G.C. Daily, H.K. Gibbs, J.H. Helkowski, T. Holloway, E.A. Howard, C.J. Kucharik, C. Monfreda, J.A. Patz, I.C. Prentice, N. Ramankutty, and P. Snyder, "Global Consequences of Land Use" *Science*, 309, 570-574, 2005
- [9] D. Tilman, P.B. Reich, and J.M.H. Knops, "Biodiversity and ecosystem stability in a decade-long grassland experiment" *Nature*, 441, 629-632, 2006.
- [10] J.D. Olden, N.L. Poff, M.R. Douglas, M.E. Douglas, and K.D. Fausch, "Ecological and evolutionary consequences of biotic homogenization" *Trends in Ecology and Evolution*, 19(1), 18-24, 2004.
- [11] M.L. McKinney, and J.L. Lockwood, "Biotic homogenization: a few winners replacing many losers in the next mass extinction" *Trends in Ecology and Evolution*, 14(11), 450-453, 1999.
- [12] J.D. Olden, and T. P. Rooney, "On defining and quantifying biotic homogenization" *Global Ecology and Biogeography*, 15, 113-120, 2006.
- [13] D.S. Srivastava, and M. Vellend, "Biodiversity-Ecosystem Function Research: Is It Relevant to Conservation?" *Annual Review Ecology Evolution and Systematics*, 36, 267-294, 2005.
- [14] P.J. Wood, D.M. Hannah, and J.P. Sadler, *Hydroecology and Ecohydrology: Past, Present and Future*, John Wiley & Sons, Ltd, 2007.
- [15] V. Andréassian "Waters and Forests: from historical controversy to scientific debate" *Journal of Hydrology* 291, 1-27, 2004.

- [16] J.H. Brown, T.G. Whitham, S.K.M. Ernest, and C.A. Gehring, "Complex species interactions and the dynamics of ecological systems: long-term experiments" *Science*, 293, 643-650, 2001.
- [17] M.A. Maleque, H. Ishii, and K. Maeto, "The use of arthropods as indicators of ecosystem integrity in forest management". *Journal of Forestry* 104, 113-117, 2006.
- [18] M.A. McGeoch "The Selection, testing and application of terrestrial insects as bioindicators" *Biological Review* 73, 181-201, 1998.
- [19] Y. Zhang, P.K. Barten "Water Forest Management Information System (WFMS)" *Environmental Modelling & Software* 24, 569-575, 2009.
- [20] V. Andréassian "Waters and Forests: from historical controversy to scientific debate" *Journal of Hydrology* 291, 1-27, 2004.
- [21] F. Imaizumi, R.C. Sidle, and R. Kamei "Effects of forest harvesting on the occurrence of landslides and debris flows in steep terrain of central Japan" *Earth Surface Processes and Landforms* 33, 827-840, 2008.
- [22] P.D. Brooks, and E.R. Vivoni "Mountain ecohydrology: quantifying the role of vegetation in the water balance of montane catchments" *Ecohydrology* 1, 187-192, 2008.
- [23] J.J. Armesto, L. Lobos, and M.K. Arroyo. 1996. Los bosques templados del sur de Chile y Argentina: una isla biogeográfica. In: Armesto J., Villagra'n C. and Arroyo M.K. (eds) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, Chile, pp. 23-28.
- [24] CONAF, CONAMA, BIRF, Universidad Austral de Chile, Pontificia Universidad Católica de Chile y Universidad Católica de Temuco. 1999. *Catastro y Evaluación de Recursos Vegetacionales nativos de Chile*. Proyecto CONAF, CONAMA Y BIRF.
- [25] C.E. Oyarzún, R. Godoy, A. Schrijver, J. Staelens, and N. Lust "Water chemistry and nutrient budgets in an undisturbed evergreen rainforest of southern Chile" *Biogeochemistry* 71, 107-123, 2004.
- [26] M.R. Willig, D.M. Kaufman, and R.D. Stevens, "Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis" *Annual Review Ecology Evolution and Systematics*, 34, 273-309, 2003.
- [27] P. Amarasekare, "Spatial Dynamics of Foodwebs" *Annual Review Ecology Evolution and Systematics*, 39, 479-500, 2008.
- [28] H.K. Ober, and J.P. Hayes, "Influence of forest riparian vegetation on abundance and biomass of nocturnal" *Forest Ecology and Management* 256, 1124-1132, 2008.
- [29] A.M. Ellison, M.B. Bank, B.D. Clinton, E.A. Colburn, K. Elliott, C.R. Ford, D.R. Foster, B.D. Kloeppel, J.D. Knoepp, G.M. Lovett, J. Mohan, C.M. Swan, J. Thompson, B. Von Holle, and J.R. Webster, "Loss of foundation species: consequences for the structure and dynamics of forested ecosystems" *Frontier Ecology Environment* 3(9), 479-486, 2005.
- [30] T.M. Lewinsohn, v. Novotny, and Y. Basset, "Insects on Plants: Diversity of Herbivore Assemblages Revisited" *Annual Review Ecology Evolution and Systematics* 36, 597-620, 2005.

- [31] S.E.M. Fraser, C. Dythan, and P.J. Mayhew, "Determinants of parasitoids abundance and diversity in woodland habitats" *Journal of Applied Ecology* 44, 352-361, 2007.
- [32] H. Kagata, and T. Ohgushi "Bottom-up trophic cascades and material transfer in terrestrial food webs" *Ecological Research* 21, 26-34, 2006.
- [33] J. Karimzadeh, and D.J. Wright, "Bottom-up cascading effects in a tritrophic system: interactions between plant quality and host-parasitoid immune responses" *Ecological Entomology*, 33, 45-52, 2008.
- [34] J.L. Pearce, and L.A. Veiner, "The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review" *Ecological Indicators* 6, 780-793, 2006.
- [35] J.B. Whitfield "Phylogeny and Evolution of Host-Parasitoid Interactions in Hymenoptera" *Annual Review Entomology* 43, 129-151, 1998.
- [36] K.J. Gaston, "The magnitude of global insect species richness", *Conservation Biology*. 5, 283-296, 1991.
- [37] J. La Salle, and I.D. Gauld. *Hymenoptera and Biodiversity*. CAB International, Wallingford, UK, 1993.
- [38] H. Gibb, and D.F. Hochuli, "Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages" *Biology Conservation* 106, 91-100, 2002.
- [39] M.R. Shaw, and M.E. Hochberg, "The neglect of parasitic Hymenoptera in insect conservation strategies: the British fauna as a prime example" *Journal of Insect Conservation*. 5, 253-263, 2001.
- [40] J. Brodeur, and G. Boivin, "Functional Ecology of Immature Parasitoids" *Annual Review Entomology* 49, 27-49, 2004.
- [41] T. Hance, J. van Baaren, P. Vernon, and G. Boivin, "Temperatures on Parasitoids in a Climate Change Perspective" *Annual Review Entomology*, 52, 107-126, 2007.
- [42] G.E. Likens, and F.H. Bormann.. *Biogeochemistry of a Forested Ecosystem*. Second Edition. Springer-Verlag. 159Pp, 1995.
- [43] S.E.M. Fraser, C. Dythan, and P. Mayhew, "The effectiveness and optimal use of Malaise traps for monitoring parasitoid wasps" *Insect Conservation and Diversity*. 1, 22-31, 2008.
- [44] C. George, and L.F. Leon. "WaterBase: SWAT in an open source GIS" *The Open Hydrology Journal* 1, 19-24, 2007.
- [45] S.L. Neitsch, J.G. Arnold, J.R. Kiniry, and J.R. Williams. *Soil and Water Assessment Tool Theoretical Documentation and User's Manual*, Version 2005, GSWR Agricultural Research Service & Texas Agricultural Experiment Station, Temple Texas, 2005.
- [46] R. Srinivasan, and J.G. Arnold. 1994 "Integration of a Basin-Scale Water Quality Model with GIS" *Water Resources Bulletin* 30(3), 453-462, 1994.
- [47] D. Tarboton, and D. P. Ames. 2001. Advances in the mapping of flow networks from digital elevation data. In *World Water and Environmental Resources Congress*. ASCE, May. See: <http://hydrology.neng.usu.edu/taudem/>

- [48] SRTM. DEM data from International Centre for Tropical Agriculture (CIAT), available from the CGIAR-CSI SRTM 90m (Database: <http://srtm.csi.cgiar.org>), 2004.
- [49] H. Taki, B.F. Viana, P.G. Kevan, F.O. Silva, and M. Buck, “Does forest loss affect the communities of trap-nesting wasps (Hymenoptera: Aculeata) in forests? Landscapes vs. local habitat conditions” *Journal Insect Conservation* 12, 15-21, 2008.

Terrestrial nitrogen cycling in southern Chile: looking back and forward

Dries Huygens¹, Pascal Boeckx²

¹Instituto de Ingeniería y Suelos, Universidad Austral de Chile, Casilla 567, Valdivia, Chile, Email: dries.huygens@ugent.be

²Laboratory of Applied Physical Chemistry - ISOFYS, Ghent University, Coupure links 653, B-9000 Ghent, Belgium, Email: pascal.boeckx@ugent.be

Abstract. The temperate climate region of southern Chile still reflects undisturbed, pre-industrial environmental conditions. This is in strong contrast with land use, which has been altered significantly over the last decades and centuries. Only fragments of the original forest vegetation remain unaltered, and are located in the coastal and Andes mountain range. Exotic tree plantations and agricultural areas dominate the central valley of southern Chile. These observations make this region an ideal study area to investigate human impacts on biogeochemical nutrient cycling. Nitrogen (N) cycling in terrestrial ecosystems is of global environmental concern. The N cycle is a complex interplay where abiotic and microbiological processes interact to transform and transfer N in an ecosystem. In general, one can simplify by classifying terrestrial N cycles all over the world in two groups: ‘tight’ N cycles and ‘open’ N cycles. The ‘tight’ N cycle is characterized by its high efficiency in producing bioavailable N and retaining it in the plant-soil system. The ‘open’ N cycle, on the other hand, is considered to be less efficient, showing significant loss of N towards aquatic ecosystems and the atmosphere. The latter losses might lead to adverse effects on stream water and air quality, contributing as such to ‘global change’. We document some results of a 10 year lasting journey of bilateral projects in several South Chilean forests. We will give insights in the ‘pristine, undisturbed’ N cycle, and evaluate disturbance impacts on the microbiological community composition, associated N transformations, and N leaching.

1. Introduction

1.1. Importance of studying N biogeochemistry in south Chilean forests

Southern Chile possesses almost one-third of the world’s few remaining large tracks of temperate forests [1]. Chile’s forests are some of the most impressive in the world, ranging from Chilean palm forests and *Scerophyllous* forests in north-central Chile, to prehistoric *Araucaria* forests, temperate rainforests, and *Alerce* forests in the South. Virtually every type of temperate forest native to the southern hemisphere can be found in Chile [2]. These forests are of great ecological, conservation and evolutionary value. They are geographically isolated from other forest formations, limiting the exchange of fauna and flora between Chilean forests

and those outside the country. Temperate forests contain a wide array of unique species, including many tree species that are endemic either to Chile or to the southern cone of South America [3]. They store vast quantities of organic matter that can contribute to control flooding, purify water, cycle nutrients, and house an incredible array of species that provide the genetic material for valuable new products and a foundation for the resilience of natural ecosystems. These are some of the most productive forests in the world [3].

The degree of nitrogen (N) input into forests is crucial for sustainable ecosystem functioning. Nitrogen is a key element controlling species composition, diversity, dynamics, functioning and vitality of forest ecosystems. A ‘classical’ N cycling approach is mainly oriented towards research performed in the relatively contaminated northern hemisphere. Many European and northeastern North American forests are subjected to enhanced N deposition, leading initially to an increased productivity and C sequestration [4]. However, when N inputs exceed the demand or storage capacity, nutrient and cation leaching occurs leading to forest decline and negatively affecting downstream water quality. Increasing N availability changes the rates and pathways of N cycling and N loss [5]. Hence, as N availability and human disturbance influence to a large extent the functioning of the microbial community, an ‘alternative’ N cycle is expected in pristine forest ecosystems. As with any global change effect, it is crucial to evaluate - if possible - the state of the N cycle prior to potential extensive human alteration. Studies in unpolluted mature ecosystems may provide us with suchlike valuable baseline information [6]. In order to understand, model and predict the consequences of future and past N deposition on ecosystem sustainability, a thorough study of forest N cycling in pristine ecosystems is crucial.

The precipitation chemistry in southern Chile is thought to reflect natural rather than anthropogenic processes. Precipitation characterization indicated that this region is one of the closest approximations of pre-industrial atmospheric conditions in the world [6, 7]. Prevailing westwards oriented winds, originating from the Pacific Ocean, are the main source of nutrient input [8]. Moreover, the pristine nature and old age of the temperate rainforests in southern Chile reflect little or no bias to human activities, indicating a unique opportunity to provide valuable ‘baseline’ information on patterns of biogeochemical N cycling [6].

1.2. The nitrogen cycle

An excellent overview of a ‘classical’ N cycle is given in Schimel *et al.* [9] (Fig. 1). This biogeochemical N cycle can be divided in external and internal N transformation processes. The external processes include pathways that add or remove N from the soil N pool, such as N deposition, biological N₂ fixation, denitrification, ammonia volatilization and N leaching [10]. Internal N transformations determine the N availability to plants and microbial community, and include decomposition, mineralization, immobilization, nitrification and

assimilation [11]. Hence, the N cycle is a complex interplay where abiotic and microbiological processes interact to transform and transfer N in an ecosystem. In general, one can simplify by classifying terrestrial N cycles all over the world in two groups: ‘tight’ N cycles and ‘open’ N cycles. The ‘tight’ N cycle is characterized by its high efficiency in producing bioavailable N and retaining it in the plant-soil system. The ‘open’ N cycle, on the other hand, is considered to be less efficient, showing significant loss of N towards aquatic ecosystems and the atmosphere.

Microorganisms involved in external N transformations are often active in a highly defined physiological pathway and are therefore indicated as physiologically ‘narrow’ [9]. The nitrification process acts as a “gatekeeper” between the internal N cycle and N output via denitrification and leaching [9]. Internal N transformation processes are postulated to be to a small extent sensitive to microbial community composition [12] and are indicated as ‘broad processes’ [9].

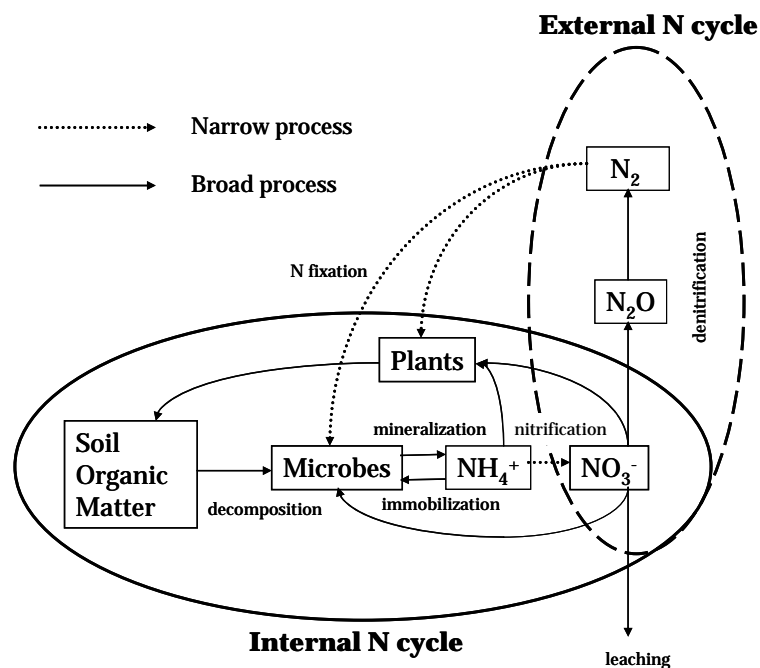


Fig. 1. Overview of the nitrogen cycle as described by Schimel *et al.* [9]

Not all N transformation reactions are mediated by soil microorganisms. Abiotic processes might contribute to a highly variable extent in forest soils, constituting 6-90% of the occurring immobilization reactions [13]. Reactions include NH_4^+ sorption/desorption reactions to clay minerals [14], exchange reactions of NO_3^- [15,16], adsorption of dissolved organic N (DON) compounds [17], and nitration/nitrosation reactions of NO_3^- [18,19]. The extent at which abiotic N transformation processes take place is only marginally affected by external N loads [13].

1.2. The use of stable isotopes to study N transformations

An isotope is a nuclide with the same number of protons in the nucleus as another nuclide, but with a different number of neutrons. Lots of chemical elements possess stable isotopes, such as hydrogen (^1H and ^2H), carbon (^{12}C and ^{13}C), oxygen (^{16}O and ^{18}O) and nitrogen (^{14}N and ^{15}N). These occur in natural environments. Stable isotopes prove to be a handy tool in the analyses of important physiological and ecological processes. Their non-radioactivity guarantees no health risks and can consequently be used in experiments carried out over extended time periods [11].

Isotopic dilution is an analytical technique for the determination of N transformation rates. Through addition of isotopically enriched substances (e.g. $^{15}\text{NO}_3^-$, $^{15}\text{NH}_4^+$, etc.) to the system under research, one can identify simultaneously occurring gross N transformation rates and obtain quantitative information on N pathways in ecosystems. For the study of a process, one pool is considered with in- and outflows. The inflow affects both the ^{15}N enrichment and the N content of the pool, because the inflowing N has a much lower ^{15}N content than the ^{15}N labelled pool. The outflow only affects the N content of the pool as the pool is completely mixed and the behaviour of ^{14}N and ^{15}N is the same [20]. As such, the dilution of ^{15}N in the labelled pool over a period of time gives an idea on the production rate of the labelled pool. Simultaneously, the outflow of ^{15}N from the labelled pool can be traced towards other N pools (e.g. leaching water, gaseous N forms, etc.) to track the fate of the labelled material (^{15}N tracing experiments).

2. The N cycle in pristine forest ecosystems

We present results of a study site located in the Andean mountain range, Antillanca, southern Chile ($40^\circ 47'\text{S}$, $72^\circ 12'\text{W}$). The site is located at 900 m a.s.l. The vegetation is characterized as a *Nothofagus betuloides* forest type [21] with an average tree age of 325 years, a stand density of 865 trees ha^{-1} , a mean tree height of 23 m, and a canopy cover of 69%. The average annual temperature is 4.5°C , while mean annual precipitation amounts to about 7000 mm. Total annual bulk N deposition equals $11.8 \text{ N kg ha}^{-1}$, from which 8.2 kg N ha^{-1} is in the form of DON, and 3.6 kg N ha^{-1} as DIN [22]. It has been proven that this mountain forest is very efficient in trapping nutrients from clouds and fog [22]. In cloud or fog dominated mountain regions, ecosystem hydrology and nutrient dynamics are closely linked to occult precipitation [23]. The soil is classified as a Umbric Vitric Andosol [IUSS Working Group WRB, 24]. This soil type has typical variable charge characteristics as a result of their particular clay mineral and organic matter content [25, 26]. In the south Chilean Andes mountain range, *Nothofagus* evergreen forest ecosystems are situated principally on geological substratum of volcanic rocks [27].

In a first stage, a ^{15}N tracing model was set up to reveal process specific NH_4^+ and NO_3^- transformation pathways [28]. Nitrogen-15 tracing studies represent the current “state-of-the-art” technique to identify simultaneously occurring gross N transformation rates and to obtain quantitative information on N fluxes in ecosystems. Tracing models are based on laboratory experiments, and used for data analysis which contains all important N pools and N transformations of the particular ecosystem. In this study, gross N transformation rates were quantified with a ^{15}N tracing model in combination with a Markov chain Monte Carlo sampling algorithm for parameter estimation. The ^{15}N tracing model included five different N pools (NH_4^+ , NO_3^- , labile (N_{lab}) and recalcitrant (N_{rec}) soil organic matter and adsorbed NH_4^+), and ten gross N transformation rates. The N dynamics in the ecosystem are characterized by low net but high gross mineralization rates. Mineralization was dominated by turnover of N_{lab} , while immobilization of NH_4^+ predominantly entered the N_{rec} pool. A fast exchange between the NH_4^+ and the adsorbed NH_4^+ pool was observed, possibly via physical adsorption on and release from clay lattices, providing an effective buffer for NH_4^+ . Moreover, high NH_4^+ immobilization rates into the N_{rec} pool ensure a sustained ecosystem productivity. Nitrate, the most mobile form of N in the system, is characterized by a slow turnover and was produced in roughly equal amounts from NH_4^+ oxidation and heterotrophic nitrification. This study showed for the first time that dissimilatory nitrate reduction to ammonium (DNRA) is mainly responsible for NO_3^- consumption in this soil.

In a second stage, we extended the ^{15}N tracing model by including NO_2^- dynamics [29]. More specifically, we fully explored the functional role of DNRA and NO_2^- turnover processes by considering concentration and isotope measurements of nitrite (NO_2^-), an intermediate of many N transformation processes. The updated ^{15}N tracing model consisted of 9 N pools and 16 N transformations (Table I). The inclusion of NO_2^- dynamics allows a more precise quantification of gross N transformation rates in this ecosystem, and thus updates the previously obtained results. We found that NO_2^- was mainly produced via NH_4^+ oxidation, but subsequently reduced rather than further oxidized to NO_3^- . This is the first time that a functional link between NH_4^+ oxidation and NO_2^- reduction in such an ecosystem has been shown and indicates that processes such as nitrifier-denitrification, chemo-denitrification, nitrosation reactions or anammox could be important processes in the *Nothofagus* soil. Heterotrophic nitrification, mainly oxidizing recalcitrant SOM, is the dominant NO_3^- production process in this soil. Furthermore, tracing analysis revealed a tight functional link between heterotrophic nitrification and DNRA. The production of NH_4^+ via the latter pathway was approximately 10 times higher than direct mineralization from recalcitrant SOM to NH_4^+ . Moreover, the rate of DNRA was several magnitudes higher than the rate of NO_3^- reduction, which confirms that denitrification is not an important pathway for N loss in this ecosystem. We argue that the functional links we identified have developed in response to the prevailing climatic conditions of this *Nothofagus* ecosystem to maintain ecosystem productivity and minimize N losses. We provide strong evidence that including NO_2^- dynamics in ^{15}N tracing studies provides new insights into the soil N cycle.

Table I. Description of model parameters and optimized values (mean and standard deviation) using a Markov chain Monte Carlo (MCMC) method, and average N transformation rates (mean and standard deviation) for a pristine south Chilean *Nothofagus* forest soil, as adopted from Huygens et al. [29].

Trans- formation	Description	Kinetics [units]*	parameter value		N rate [$\mu\text{g g}^{-1} \text{d}^{-1}$]	
			mean	stdev	mean	stdev
$I_{NH_4^+ N_{lab}}$	Immobilization of NH_4^+ to N_{lab}	0 [$\mu\text{mol g}^{-1} \text{h}^{-1}$]	0.00157	0.00002	0.528	0.007
$I_{NH_4^+ N_{rec}}$	Immobilization of NH_4^+ to N_{rec}	0 [$\mu\text{mol g}^{-1} \text{h}^{-1}$]	0.00797	0.00024	2.681	0.082
$I_{NO_3^-}$	Immobilization of NO_3^- to N_{rec}	0 [$\mu\text{mol g}^{-1} \text{h}^{-1}$]	0.00002	0.00000	0.006	0.001
$M_{N_{rec}}$	Mineralization of N_{rec} to NH_4^+	0 [$\mu\text{mol g}^{-1} \text{h}^{-1}$]	0.00012	0.00006	0.039	0.021
$M_{N_{lab}}$	Mineralization of N_{lab} to NH_4^+	1 [h^{-1}]	0.00018	0.00004	3.690	0.828
$O_{NH_4^+}$	Oxidation of NH_4^+ to NO_2^- nit	1 [h^{-1}]	0.00005	0.00000	0.665	0.023
$O_{N_{rec}}$	Oxidation of N_{rec} to NO_3^- org	0 [$\mu\text{mol g}^{-1} \text{h}^{-1}$]	0.00127	0.00005	0.428	0.016
$D_{NO_3^-}$	Dissimilatory NO_3^- reduction to NH_4^+	0 [$\mu\text{mol g}^{-1} \text{h}^{-1}$]	0.00106	0.00005	0.355	0.016
$A_{NH_4^+}$	Adsorption of NH_4^+ to NH_4^+ ads	1 [h^{-1}]	0.00328	0.00020	40.285	2.453
$R_{NH_4^+ ads}$	Release of adsorbed NH_4^+ to NH_4^+	1 [h^{-1}]	0.00463	0.00032	42.674	2.987
$O_{NO_2^- nit}$	Oxidation of NO_2^- nit to NO_3^-	1 [h^{-1}]	0.00282	0.00042	5.5E-05	8.3E-06
$O_{N_{org}}$	Oxidation of N_{rec} to NO_2^- org	1 [h^{-1}]	3.7E-07	7.8E-09	0.044	0.001
$R_{NO_3^-}$	Reduction of NO_3^- to NO_2^- den	1 [h^{-1}]	7.7E-08	2.4E-08	1.6E-05	4.8E-06
$R_{NO_2^- nit}$	Reduction of NO_2^- nit to N_{gas}	1 [h^{-1}]	34.76489	0.36870	0.677	0.007
$R_{NO_2^- den}$	Reduction of NO_2^- den to N_{gas}	1 [h^{-1}]	0.04728	0.01604	1.9E-05	6.5E-06
$R_{NO_2^- org}$	Reduction of NO_2^- org to N_{gas}	1 [h^{-1}]	0.06168	0.00079	0.044	0.001

Previously obtained results were validated in the field via a “ ^{15}N pulse chase study” [30]. A combination of field ^{15}N isotope dilution and ^{15}N tracer techniques was used to study N transfer between soil, water and vegetation compartments. This field study confirms our previous observations obtained in laboratory experiments that N-limited evergreen forest ecosystems in areas of high rainfall develop efficient mechanisms for N supply and at the same time avoid N losses. It is indicated that the forest retained a large proportion of NO_3^- and NH_4^+ added in the long term (~ 1 year). We confirmed that heterotrophic nitrification dominates (96%) total NO_3^- production. In addition to N mineralization, DNRA is a significant NH_4^+ production pathway in this forest soil. Moreover, it was found that DIN is retained in the soil

via immobilization into SOM, or turn over into hydrophobic soluble organic N (SON), an organic soil N pool that shows a high sorption affinity. It is indicated that the documented DON leaching losses do not originate from DIN turnover; DON flows are controlled by soil dynamics that operate independently from DIN turnover.

We aim to refine the proposed N cycling paradigm of Schimel and Bennett [31] for evergreen rainforest ecosystems in temperate climates via the inclusion of heterotrophic nitrification and DNRA. These coupled pathways explain transformation of recalcitrant SOM compounds into NH_4^+ , without inducing N losses. Hence, heterotrophic nitrification and DNRA complement N mineralization, and ensure ecosystem productivity via continuous formation of bioavailable N for the microbial community and plants, without concomitant inorganic N losses. A final conceptual model for the N cycle in volcanic soils of temperate rainforests is given in Fig. 2.

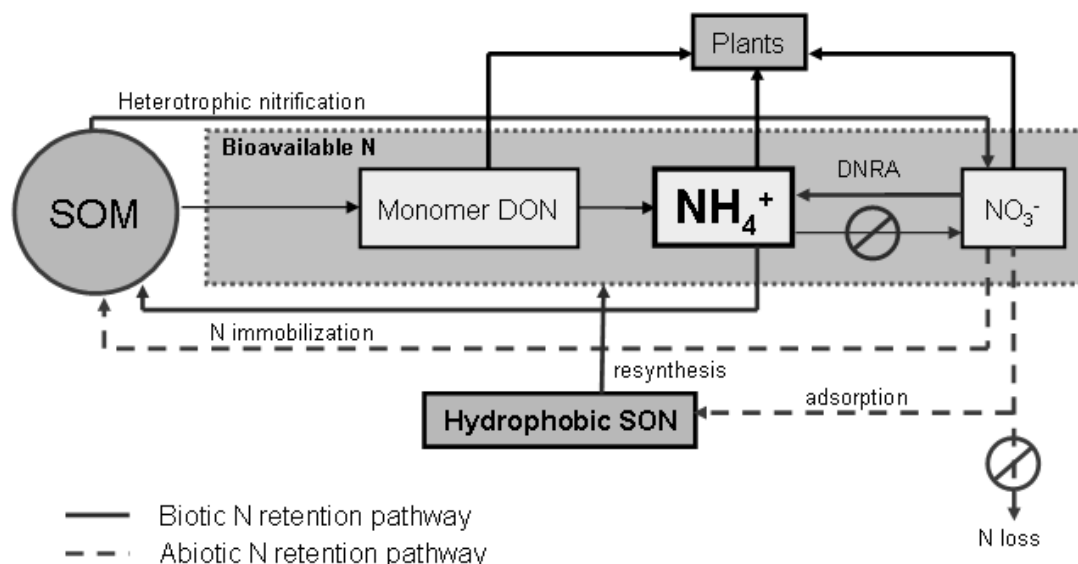


Fig. 2. Conceptual model for the nitrogen (N) cycle in volcanic soils of temperate rainforests (DON=dissolved organic N, DNRA=dissimilatory nitrate reduction to ammonium, SOM=soil organic matter, SON=soluble organic N) (adopted from Huygens et al. [30])

3. The effect of ecosystem disturbance on the N cycle

3.1. Land use conversion

In contrast to findings from forests in polluted regions, stream water NO_3^- concentrations in unpolluted native forests of South America, experiencing minimal N pollution and minimal disturbances from logging and other human activities, are exceedingly low and dissolved organic N is responsible for the majority of N losses

[32]. Land use conversion, in particular replacement of forests by agriculture or pasture land, strongly influences watershed nutrient fluxes [33]. The effect on N export of converting native temperate forests to fast-growing exotic plantations is poorly understood. This substitution of native vegetation is associated with rather drastic logging practices with a possible impact on stream water quality through biomass removal, a variable quantity of logging slash on the forest floor, soil erosion and accelerated N mineralization [e.g. 34].

To study the effect of land-use conversions on N losses, Oyarzún et al. [35] selected six catchments with relatively homogeneous physiography, geology, climate and soil, distributed over a total area of 3,321 ha (Table II). The catchments were located at the Cordillera de la Costa (39° 50'–40° 05' S and 73° 10'–73° 20' W) near the city of Valdivia, with an elevation ranging between 5 and 700 m a.s.l. The climate is humid temperate. The annual rainfall increases with altitude, from about 2,000 mm near the coast to approximately 6,000 mm at the top of the Coastal Range.

Table II. Soil and land-use characteristics for the catchments at the Cordillera de la Costa in southern Chile, as adopted from Oyarzún et al. [35]

Catchment	Code	Size ha	Altitude m	Soil Series	Native Forest (%)	Plantation (%)	Shrub (%)	Pasture (%)
San Juan	SJU	1462	5–700	Hueycolla–Los Ulmos	91.6	0.0	7.4	0.4
Las Minas	LMI	884	5–575	Hueycolla–Los Ulmos	67.8	13.6	14.0	4.3
Guindos	GUI	252	25–400	Los Ulmos	70.0	22.0	6.0	0.0
Joaquines	JOAQ	282	45–560	Los Ulmos	46.6	33.1	13.6	5.2
La Plata	LPL	386	75–255	Los Ulmos	18.9	62.5	18.0	0.3
Joaquines 2	JOA2	55	45–400	Los Ulmos	6.8	76.0	13.6	0.0

The results showed that NO_3^- concentrations in stream-water in the catchment dominated by native forests were lower than concentrations in the catchments partially covered by exotic plantations of *Pinus radiata* and *Eucalyptus* sp. In five catchments partially covered by exotic plantations, the $\text{NO}_3\text{-N}$ fraction amounted to more than 50%, while in the catchment with native forest, NO_3^- contributed 34% to the total nitrogen loss. Only in the catchment with native forest, DON accounted for the dominant fraction of N loss. This suggests an ‘opening’ of the N cycle by forest conversion to exotic tree plantations. Total N retention was positively related with native forest coverage. Therefore, differences in N retention capacity among catchments can be related to vegetation cover and possibly consequences of logging practices. Some data from more polluted areas located in the Northern Hemisphere show that vegetation plays an important role in regulating N losses from watersheds. In this study, under a low deposition climate, the results indicate that conversion of native forests to exotic fast growing plantations is likely to decrease N retention.

About 150 years ago, most parts of the Chilean Central Valley were dominated by forest stands. However, European colonization significantly altered the main land use of this region. Former human practices may persistently affect microbial communities and the processes they mediate both directly and indirectly. Direct effects of past land use may occur via long-term (>50 yr) physical alteration of the rhizosphere caused by historic practices. Soil compaction is an enduring consequence of cultivation, grazing, and logging that can cause increased bulk density and reduced pore space. These changes may affect the abundance of aerobic and anaerobic microorganisms and subsequently reduce the cycling of several elements, including N (Waldrop et al. 2000, Cleveland et al. 2003). Huygens et al. (unpublished) investigated the microbial community abundance and composition of different sites located in southern Chile, and tried to link the obtained results to N biogeochemistry. Four areas in southern Chile were studied in order to get a clearer insight on this subject. All four sites are characterised by a volcanic soil (Andisol) but have different land use and N-input. The four sites include two different agricultural sites with higher N-fertilization and two different forest sites with low N-input. The two agricultural sites are located near the city Osorno. The first, Remehue, is a cultivated land with approximately $180 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ of fertilization. The second, La Pampa, has a history of pasture land and less N fertilization (approximately $40 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). The two forest sites are located in the old-growth forest in Parque Nacional Puyehue near the Andean mountain range, a ‘Valdivian forest’ at 500 m a.s.l. and a ‘*Nothofagus betuloides*’ forest at 750 m a.s.l. Both are characterised by evergreen trees and high precipitation.

Results indicate that the total microbial biomass concentrations varied according to the topo-land-use-sequence. The forest sites showed the highest concentrations, while a decrease was visible from the *N. betuloides* forest to the agricultural sites. The lowest concentration was, however, noticed at La Pampa and not at the highly fertilized field of Remehue. The influence of pesticides, tillage and high N fertilization could have caused a significant decrease in the microbial biomass. The microbial community structure of the agricultural sites was characterised by a high relative abundance in gram-positive bacteria and actinomycetes. The forest sites on the other hand had high relative abundances in gram-negative bacteria and fungi. The higher microbial activities are also translated in higher N transformation rates in the forest stands. Statistical analysis packets indicated a functional link between microbial community structure and N transformations. Hence, we can conclude that former land use changes significantly altered the microbial community composition, which in turn alters biogeochemical N fluxes.

3.2. Wildfire

Heavy ecosystem disturbance events, such as wildfires, have the potential to cause abrupt changes in N transformation rates and induce ecosystem N losses. Beside to losses to the atmosphere, biological and non-biological processes after burning are known to transform organic N forms into more available ammonium, nitrate and dissolved organic matter [36].

Between December 2001 and February 2002 ca. 20,000 ha of the Parque Nacional Tolhuaca (38°10'S, 71°40'W to 38°15'S, 71°50'W at ca. 1.200 m a.s.l.) in southern Chile was affected by a severe, stand removing, wildfire. The latter temperate rainforest was dominated by endemic tree species such as *Araucaria araucana* (Mol) K. Koch and *Nothofagus* sp. Several studies (Paulino et al., unpublished; Rivas et al. unpublished) assessed changes in N cycling as a result of fire by studying burned and unburned soil plots in the National Park 'Tolhuaca'. Stable isotope analyses indicated that fire intensified gross NO_3^- and NH_4^+ production. The burned sites showed a marked increase in the standing pool N size after the fire. In June 2003, the NO_3^- contents in the 0-20 and 20-40 cm depth profiles increased up to ca. 60 and 30 $\mu\text{g NO}_3^-\text{-N g}^{-1}$, respectively. Moreover, NO_3^- concentrations in river water discharging from the burned site reached concentrations of up to ca. 3.5 mg $\text{NO}_3^-\text{-N L}^{-1}$ immediately after the wildfire, decreasing to background concentrations ($< 10 \mu\text{g NO}_3^-\text{-N L}^{-1}$) only 3 years after the fire event. We hypothesized that the availability of 'black carbon' increases available NO_3^- concentration by stimulating the autotrophic nitrification process. As such, an excess concentration of plant available nutrients is available in the soil matrix after fire, enhancing further N losses via soil leaching.

4. Conclusion

Our studies revealed that pristine forest ecosystems show a tight N cycle via specific N transformation processes, such as DNRA and heterotrophic nitrification. Specialist microorganisms are involved in these N transformations, and assure as such sustainable N functioning and prevent ecosystem N losses. We indicated that microbial community composition and associated N transformation rates are susceptible to various forms of ecosystem disturbance. The latter disturbance effects induced 'an opening' of the N cycle, leading to significant N losses. In the long-term, quantitative and qualitative changes in ecosystem N cycling may affect botanical diversity, ecosystem N losses, and net primary productivity of the ecosystem. For these reasons, it is necessary to investigate how sensible existing microbial communities, and their associated N transformations, are to future stress factors (climate driven variability, intensification of agricultural activities in the region increasing atmospheric N loads, etc.).

Acknowledgement

This research was supported by various organizations such as the National Commission for Scientific and Technological Research - Chile (FONDECYT, Project N°1090455), the Bilateral Scientific and Technological Cooperation between Flanders and Chile (BOF, UGent), and the Fund for Scientific Research - Flanders (FWO).

References

- [1] D. Bryant, D. Nielsen, and L. Tangle, *Las ultimas fronteras forestales: Ecosistemas economías en el límite*. World Resources Institute, Washington, D.C., USA, 1997.
- [2] A. Lara, M.E. Solari, P. Rutherford, O. Thiers, R. Trecaman, R. Molina, R. Prieto, and C. Monory, *Cobertura de la vegetación original de la Ecoregión de los bosques valdivianos en Chile hacia 1550. Informe Técnico, Proyecto FB 19-WWF/Universidad Austral de Chile, Valdivia, Chile, 1999.*
- [3] E. Neira, H. Verscheure, and C. Revenga, *Chile's frontier forests: conserving a global treasure*. World Resources Institute - Global forest watch, Valdivia, Chile, 2002.
- [4] P.M. Vitousek, and R.W. Howarth, "Nitrogen limitation on land and in the sea - how can it occur" *Biogeochemistry*, 13, 87-115, 1991.
- [5] J.D. Aber, A. Magill, S.G. McNulty, R.D. Boone, K.J. Nadelhoffer, M. Downs, and R. Hallett, "Forest biogeochemistry and primary production altered by nitrogen saturation" *Water Air and Soil Pollution*, 85, 1665-1670, 1995.
- [6] L.O. Hedin, J.J. Armesto, and A.H. Johnson, "Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory" *Ecology*, 76, 493-509, 1995.
- [7] J.N. Galloway, W.C. Keene, and G.E. Likens, "Processes controlling the composition of precipitation at a remote southern hemispheric location: Torres del Paine National Park, Chile" *Journal of Geophysical Research-Atmospheres*, 101, 6883-6897, 1996.
- [8] T.T. Veblen, and P.B. Alaback. A comparative review of forest dynamics and disturbance in the temperate rainforests of North and South America. In: R.G. Lawford, P.B. Alaback, and E. Fuentes (Eds.), *High latitude rain forests and associated ecosystems of the west coast of the Americas: Climate, hydrology, ecology and conservation*, Vol, 116, Springer-Verlag, New York, 1996.
- [9] J.P. Schimel, J. Bennett, and N. Fierer. Microbial community composition and soil nitrogen cycling; is there really a connection. In: R.D. Bardgett, M.B. Usher, and D.W. Hopkins (Eds.), *Biological diversity and function in soils*, Cambridge University Press, Cambridge, UK, 2005.
- [10] M. Aubert, F. Bureau, and M. Vincelas-Akpa, "Sources of spatial and temporal variability of inorganic nitrogen in pure and mixed deciduous temperate forests" *Soil Biology & Biochemistry*, 37, 67-79, 2005.
- [11] F.J. Stevenson, and M.A. Cole, *Cycles of soil. Carbon, nitrogen, phosphorus, sulfur, micronutrients*. John Wiley & Sons Inc., New York, 1999.
- [12] J.P. Schimel. Ecosystem consequences of microbial diversity and community structure. In: F.S. Chapin, and C. Korner (Eds.), *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences*, Springer-Verlag, Berlin, Germany, 1995.

- [13] D.W. Johnson, W. Cheng, and I.C. Burke, "Biotic and abiotic nitrogen retention in a variety of forest soils" *Soil Science Society of America Journal*, 64, 1503-1514, 2000.
- [14] H. Nömmik, and K. Vahtras. Retention and fixation of ammonium and ammonia in soils. In: S.J. Stevenson (Ed.) *Nitrogen in agricultural soils*, ASA-CSSA-SSSA, Madison, WI, 1982.
- [15] K.C. Cameron, and R.J. Haynes. Retention and movement of nitrogen in soils. In: R.J. Haynes (Ed.) *Mineral nitrogen in plant-soil ecosystem*, Academic press, Orlando, USA, 1986.
- [16] C.A. Pérez, L.O. Hedin, and J.J. Armesto, "Nitrogen mineralization in two unpolluted old-growth forests of contrasting biodiversity and dynamics" *Ecosystems*, 1, 361-373, 1998.
- [17] K. Kaiser, and W. Zech, "Dissolved organic matter sorption by mineral constituents of subsoil clay fractions" *Journal of Plant Nutrition and Soil Science-Zeitschrift Fur Pflanzenernahrung Und Bodenkunde*, 163, 531-535, 2000.
- [18] E.A. Azhar, R. Verhe, M. Proot, P. Sandra, and W. Verstraete, "Binding of nitrite-N on polyphenols during nitrification" *Plant and Soil*, 94, 369-382, 1986.
- [19] E.A. Davidson, J. Chorover, and D.B. Dail, "A mechanism of abiotic immobilization of nitrate in forest ecosystems: the ferrous wheel hypothesis" *Global Change Biology*, 9, 228-236, 2003.
- [20] D. Barraclough, "¹⁵N isotope dilution techniques to study soil nitrogen transformations and plant uptake" *Fertilizer Research*, 42, 185-192, 1995.
- [21] C. Donoso, *Ecología forestal: el bosque y su medio ambiente*. Editorial Universitaria, Santiago, Chile, 1981.
- [22] C.E. Oyarzún, R. Godoy, A. De Schrijver, J. Staelens, and N. Lust, "Water chemistry and nutrient budgets in an undisturbed evergreen rainforest of southern Chile" *Biogeochemistry*, 71, 107-123, 2004.
- [23] K.C. Weathers, "The importance of cloud and fog in the maintenance of ecosystems" *Trends in Ecology & Evolution*, 14, 214-215, 1999.
- [24] IUSS-Working-Group-WRB. 2006. World reference base for soil resources 2006 World Soil Resources Report N°103. FAO, Rome.
- [25] M. Nanzyo, R.A. Dahlgren, and S. Shoji. Chemical characteristics of volcanic ash soils. In: S. Shoji, M. Nanzyo, and R.A. Dahlgren (Eds.), *Volcanic ash soils: Genesis, properties and utilization*, Elsevier, Amsterdam, the Netherlands, 1993.
- [26] D.J. Radcliffe, and G.P. Gillman. Surface charge characteristics of volcanic ash soils from the southern highlands of Papua New Guinea. In: E.F. Caldas, and D.H. Yaalon (Eds.), *Volcanic soil*, Catena, Braunschweig, Germany, 1985.
- [27] T.T. Veblen, C. Donoso, T. Kitzberger, and A.J. Robertus. Ecology of southern Chilean and Argentinean *Nothofagus* forests. In: T.T. Veblen, R. Hill, and J. Read (Eds.), *The ecology and biography of Nothofagus forests*, Yale University Press, New Haven, Connecticut, USA., 1996.
- [28] D. Huygens, T. Rütting, P. Boeckx, O. Van Cleemput, R. Godoy, and C. Müller, "Soil nitrogen conservation mechanisms in a pristine south Chilean *Nothofagus* forest ecosystem" *Soil Biology & Biochemistry*, 39, 2448-2458, 2007.

- [29] T. Rütting, D. Huygens, C. Müller, O. Van Cleemput, R. Godoy, and P. Boeckx, "Functional role of DNRA and nitrite reduction in a pristine south Chilean *Nothofagus* forest" *Biogeochemistry*, 90, 243-258, 2008.
- [30] D. Huygens, P. Boeckx, P. Templer, L. Paulino, O. Van Cleemput, C. Oyarzún, C. Müller, and R. Godoy, "Mechanisms for retention of bioavailable nitrogen in volcanic rainforest soils" *Nature Geoscience*, 1, 543-548, 2008.
- [31] J.P. Schimel, and J. Bennett, "Nitrogen mineralization: challenges of a changing paradigm" *Ecology*, 85, 591-602, 2004.
- [32] S.S. Perakis, and L.O. Hedin, "Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds" *Nature*, 415, 416-419, 2002.
- [33] P.M. Vitousek, J.D. Aber, R.W. Howarth, G.E. Likens, P.A. Matson, D.W. Schindler, W.H. Schlesinger, and D.G. Tilman, "Human alteration of the global nitrogen cycle: Sources and consequences" *Ecological Applications*, 7, 737-750, 1997.
- [34] P.A. Matson, P.M. Vitousek, J.J. Ewel, M.J. Mazzarino, and G.P. Robertson, "Nitrogen transformations following tropical forest felling and burning on a volcanic soil" *Ecology*, 68, 491-502, 1987.
- [35] C. Oyarzun, C. Aracena, P. Rutherford, R. Godoy, and A. Deschrijver, "Effects of land use conversion from native forests to exotic plantations on nitrogen and phosphorus retention in catchments of southern chile" *Water Air and Soil Pollution*, 179, 341-350, 2007.
- [36] H. Knicker, "How does fire affect the nature and stability of soil organic nitrogen and carbon? A review" *Biogeochemistry*, 85, 91-118, 2007.

Aboveground nutrient cycling in temperate forest ecosystems of southern Chile

Jeroen Staelens^{1,2}, Carlos Oyarzún³, Leonardo Almonacid⁴, Evelyn Padilla⁴,
Kris Verheyen²

¹Laboratory of Applied Physical Chemistry (ISOFYS), Ghent University, Coupure links 653, B-9000 Ghent, Belgium. E-mail: jeroen.staelens@ugent.be

²Laboratory of Forestry, Ghent University, Geraardsbergsesteenweg 267, B-9090 Melle-Gontrode, Belgium. E-mail: kris.verheyen@ugent.be

³Institute of Geosciences, Universidad Austral de Chile, Casilla 567, Valdivia, Chile. E-mail: coyarzun@uach.cl

⁴Institute of Botany, Universidad Austral de Chile, Casilla 567, Valdivia, Chile. E-mail: leoalmonacid@gmail.com, evpadillaoy@gmail.com

Abstract. Forest ecosystems have important ecological, economic, and social values, but are subject to varying ecosystem pressures, including enhanced atmospheric nitrogen deposition. This paper quantifies nutrient fluxes in varying forest types in southern Chile in order to evaluate external and internal nutrient cycling within ecosystems, with a focus on the aboveground compartment. The objectives were to establish baseline data for pristine forest ecosystems and to study differences between forest types. Measurements were performed in four stands in the lower Andean mountain range (San Pablo de Tregua), two stands in the Central Depression (Paillaco) and six catchments in the Coastal mountain range (40°S). External nutrient inputs and losses were assessed by analyzing precipitation, throughfall, stemflow, soil percolation, and streamflow. Internal aboveground nutrient cycling was quantified by means of a canopy budget model, litterfall collection, and a litterbag decomposition experiment. Although temperate forests in southern Chile still represent a unique opportunity to study pristine ecosystems, measurements of water and ion fluxes indicate that forests in the central depression are exposed to enhanced external nitrogen inputs.

1. Introduction

1.1. Nutrient cycling in forest ecosystems

Nutrient cycling in forest ecosystems occurs at three levels of spatial scale: biochemical, biogeochemical, and geochemical cycling, as illustrated (Fig. 1). Biochemical nutrient cycling occurs within an individual organism such as a forest tree. Processes involved are upwards transport of water and dissolved nutrients taken up by roots via stem xylem, and redistribution of nutrients and sugars produced by photosynthesis to other plant parts via phloem. Redistribution within plants occurs throughout the growing season, and is an important mechanism for retaining nutrients before foliage abscission and litterfall [1]. Biochemical processes are not discussed in the present paper.

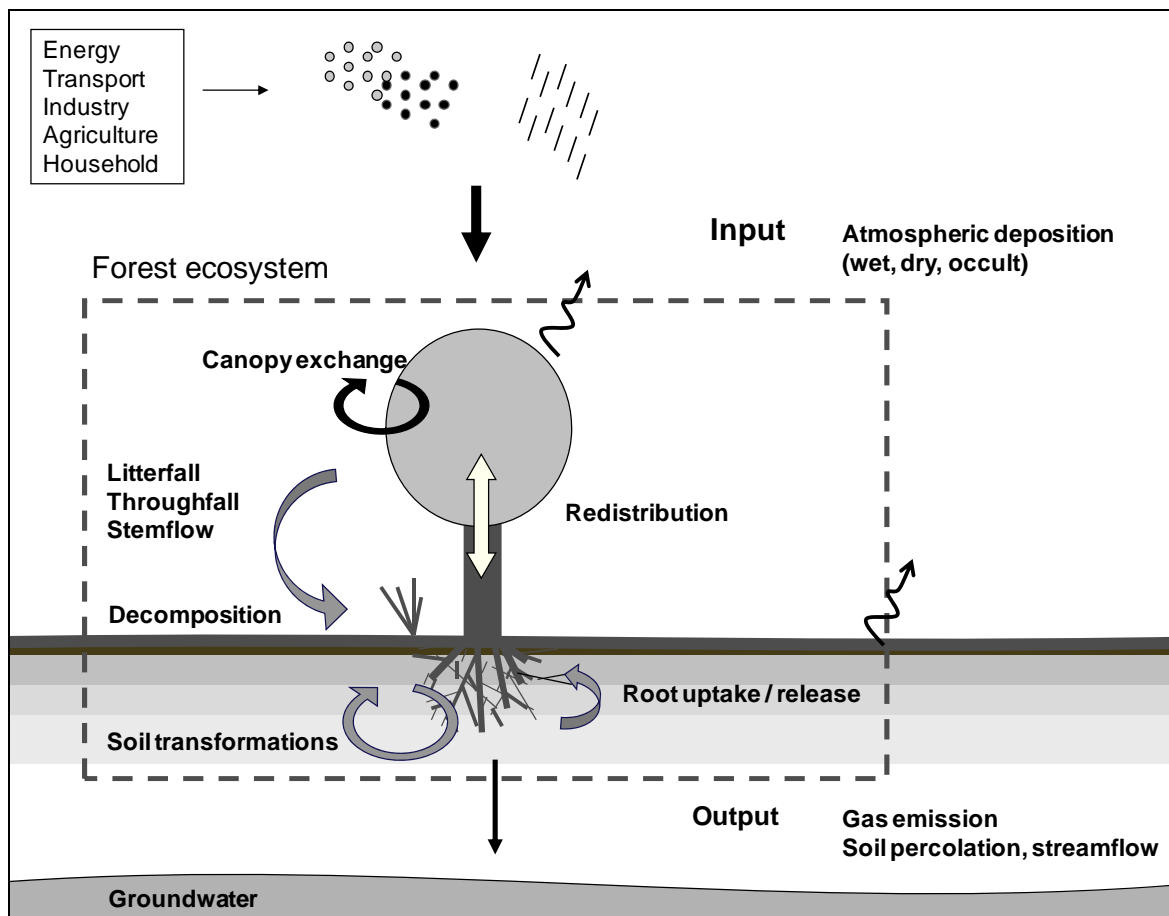


Fig. 1. Nutrient cycling in forest ecosystems. See text for a description of the main processes at the biochemical, biogeochemical, and geochemical level

Biogeochemical cycling is the internal cycling of nutrients within an ecosystem, and is governed by litterfall, decomposition, soil processes, and nutrient uptake. It should be noted that ‘ecosystem’ in this respect not only consists of the aboveground and belowground plant parts, but also of humus, organic material, animals and micro-organisms in the rooted soil layers. The term litterfall is generally used to describe the aboveground flux of dead organic material from trees and shrubs to the forest floor, and consists of leaves, needles, twigs, branches, buds, flowers, fruits, seeds, and bark. Furthermore, a large amount of dead organic material is produced belowground by the turnover of fine roots. The decomposition of aboveground and belowground organic material and subsequent release of nutrients are crucial within the internal cycling of forest ecosystems. The rate of litter decomposition can vary strongly, and is mainly governed by the interaction between climate, substrate quality, and the decomposer community. Consequently, tree species can partly affect biogeochemical cycling through the quantity and quality of the produced litter and the associated abundance and activity of soil organisms. Biogeochemical soil processes include amongst others microbial nitrogen (N) transformations such as mineralization, nitrification, and immobilization [2] and exchange of so-called base cations potassium (K^+), calcium (Ca^{2+}), and magnesium

(Mg^{2+}) between soil clay and humus and soil solution. Plants can take up nutrients from the soil solution by their roots as well as from the atmosphere by foliage and twigs. To improve water and nutrient uptake, most forest plants rely on interactions with symbiotic mycorrhizal fungi. In addition to belowground root activity, exchange of dissolved and gaseous mineral elements uptake and release of mineral elements by terrestrial plants occurs aboveground by foliage and other plant parts [3]. This process of canopy exchange is important from a biogeochemical point of view (e.g., the release of K^+ from canopy foliage to passing precipitation water) as well as from a geochemical point of view (e.g. uptake and assimilation of NO_2 from the air by the foliage).

The movement of nutrients between ecosystems is called geochemical cycling or external cycling. Two important input processes to forests are atmospheric deposition and mineral weathering. The atmospheric input to forests consists of dry, wet, and cloud deposition. Aerosols and gases can be deposited directly from the air to plant and soil surfaces during rainless periods by dry deposition. Wet deposition is defined as the input of atmospheric compounds to the earth's surface by rain, hail or snow. Occult deposition occurs via fogs and clouds, and can be important in mountainous regions [4]. During rain events, dry deposition is washed off from plant parts and, together with wet deposition, reaches the forest floor as throughfall and stemflow. Throughfall is precipitation water dripping through the canopy or directly through canopy gaps; stemflow is water reaching the forest floor via the stem bole. Because of canopy exchange processes, the total nutrient flux in throughfall and stemflow does not equal the sum of wet, dry, and occult deposition. However, the measured throughfall and stemflow nutrient flux can be combined with canopy budget models to estimate total atmospheric deposition of the major nutrients [5]. A second input process is the weathering of soil minerals as a result of chemical dissolution. In combination with atmospheric deposition, mineral weathering is the only long-term source of base cations for terrestrial ecosystems. Mineral weathering is difficult to quantify, and is not included in the present paper. At the geochemical level, most nutrients are retained within the ecosystem, but nutrient loss can occur as well. Elements can be lost under dissolved form by water percolation below the rooting zone or by gaseous emissions from forest soil (e.g. by denitrification) or canopy (e.g. volatile organic compounds, VOCs). In undisturbed natural ecosystems, the main nutrient loss is thought to consist of dissolved organic matter [6]. However, in more polluted regions, large amounts of N and base cations can be lost from forest ecosystems (cf. 1.2), and this largely occurs by soil water percolation. Nutrient losses at the geochemical level can be quantified at the plot scale by measuring nutrient fluxes below the rooting zone, or at the catchment scale by measuring nutrient fluxes in streamflow. Both approaches are used in the present paper.

1.2. Forest ecosystems and air pollution

Air pollution is caused by multiple pollutants including ammonia (NH_3), nitrogen oxides (NO_x), sulphur dioxide (SO_2), carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), particulate matter, and volatile organic compounds (VOCs), which are emitted by sources such as energy production, households, transport, agriculture, and industry. These pollutants have multiple effects on acidification and eutrophication of ecosystems, climate change, urban air quality, and tropospheric ozone. One key element in air pollution is N, although this element is essential for all life forms. Between 1860 and 2000, the production of reactive N (i.e. all active N compounds in atmosphere and biosphere other than N_2) by humans has increased worldwide from 15 Tg yr⁻¹ to approximately 165 Tg yr⁻¹ [7]. As a result, the anthropogenic production of reactive N during the last decades has been greater than the production from all natural terrestrial ecosystems. Reactive N accumulates in the environment and contributes to all contemporary environmental problems mentioned above. In addition, N accumulation leads to biodiversity loss in many natural habitats, soils, lakes, and streams [7].

Forest ecosystems are widely recognized for their important ecological, economic and social values and ecosystem services. Nevertheless, forests are subject to a variety of ecosystem pressures, such as deforestation, forest degradation, invasion of exotic species, climate change, and air pollution. Forest efficiently scavenge both gaseous and particulate pollutants from the atmosphere because of their rough surface structure, high leaf area index, and physiological characteristics of leaves and needles [8]. Consequently, the input of atmospheric dry deposition to forest canopies is often considerably enhanced compared to the dry deposition to lower vegetation types or the open field.

Atmospheric N inputs to forests have mainly been studied in Europe and NE America. Chronically enhanced N deposition has been shown to modify N soil processes and to result in varying ecosystem responses, including increased biomass growth and carbon sequestration, but also increased losses of N by emission of N oxides from soils and leaching below the rooting zone, mainly as nitrate (NO_3^-). The leaching of NO_3^- by water percolation can be substantial [9] and may lead to undesirable changes in plant availability of other essential (e.g. Ca^{2+} , Mg^{2+} , K^+) and toxic (e.g. aluminium) elements, and to soil acidification and groundwater pollution [10]. The cycling of N and other nutrients has been shown to be affected by forest type. For example, for coniferous and deciduous forest stands at comparable sites in Europe, it is known that both N deposition onto the forest floor as well as N loss by leaching below the rooting zone are significantly higher in coniferous stands [11].

1.3. Objectives

Within the framework of ten years of bilateral scientific cooperation between Universidad Austral de Chile and Ghent University (Belgium), several joint

research projects have been performed in forest ecosystems in southern Chile. As outlined above, a wide range of processes is relevant with respect to nutrient cycling, many of which have been studied in detail for forest ecosystems in the northern hemisphere. However, only little information is available about these processes in pristine forest ecosystems of southern Chile. Because of the awareness of air pollution impacts on forest ecosystems, the study focus was on the internal and external cycling of the main nutrients (N , K^+ , Ca^{2+} , Mg^{2+}). Here we shortly present results of these nutrient cycling studies, which had as main objectives to establish baseline data for pristine forest ecosystems in southern Chile and to examine differences between forest types.

2. Methods

2.1. Study areas

2.1.1. San Pablo de Tregua

Four forest stands were studied at San Pablo de Tregua ($39^{\circ}35' S$, $72^{\circ}07' W$, 600-920 m a.s.l.) located in the lower Andean mountain range, near Panguipulli in the province of Valdivia in the lake district of southern Chile (Fig. 2). The climate is temperate and rainy, with short and dry summers. Mean annual precipitation is 4000-5000 mm and mean annual temperature is $11^{\circ}C$. Soils originate from volcanic ash of different ages and are classified as Andisols (FAO classification), the local soil name being 'trumaos'. The prevailing vegetation in the area corresponds to pristine and secondary temperate forest ecosystems dominated by *Nothofagus*.

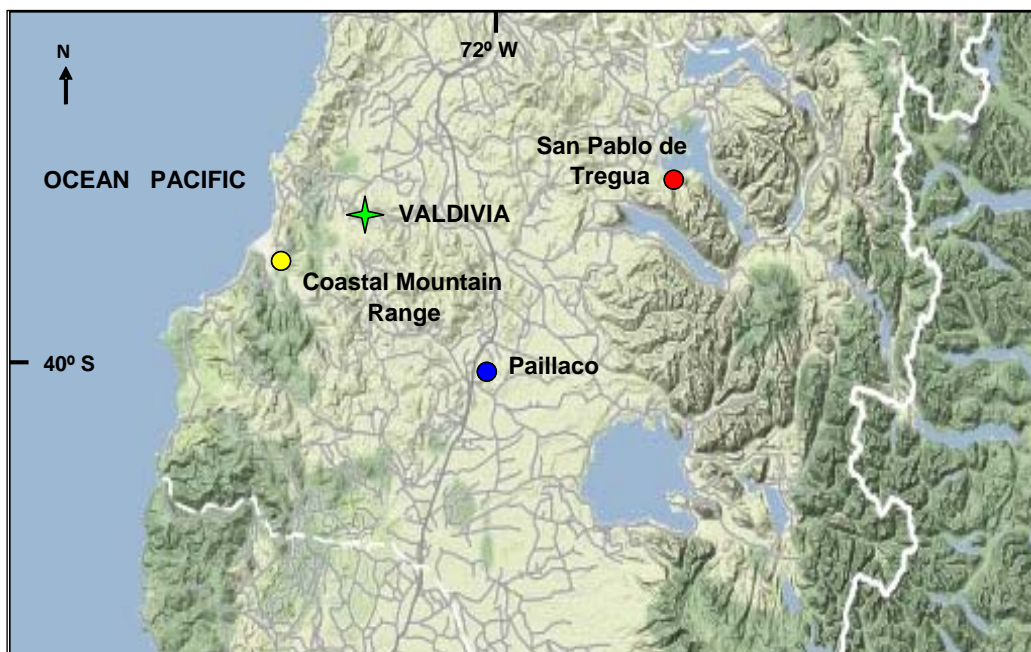


Fig. 2. Location of the three study areas in the province of Valdivia, southern Chile

In this study region, two evergreen and two deciduous forests were selected in which 1000 m² instrumented plots were established. The two plots with old-growth

evergreen forest correspond to a pristine forest (EP) and to an altered forest (EA) that has undergone an anthropogenic disturbance in 1950. Consequently, the tree composition and number of trees clearly differ, with a density of 267 and 873 trees ha⁻¹ for the EP and EA forest, respectively. The dominant tree species are *Nothofagus dombeyi* (Mirb.) Oerst., *Saxegothaea conspicua* Lindl. and *Laureliopsis philippiana* Looser. The plots with secondary deciduous forests consist of *Nothofagus alpina* (Poepp. et Endl) Oerst and *Nothofagus obliqua* (Mirb) Oerst with an age of 55-60 yr. The density of the unmanaged deciduous (DU) stand is 1300 trees ha⁻¹. In the managed stand (DM) the density is 1030 trees ha⁻¹ due to a forestry intervention in 2002, by which 35% of the basal area was taken out and the canopy cover was reduced by 40%.

2.1.2. Paillaco

Two other forest stands were selected in the province of Valdivia in southern Chile, located near Paillaco in the Central Depression (40°07'S, 72°51'W, 160 m a.s.l., Fig. 2). The climate is classified as temperate. The annual precipitation during the study period was 1187 mm and the mean annual temperature was 7°C. Soils of the area are denominated as Typic Dystrandepts (FAO classification) originating from old volcanic ash.

The stands at this site are a *N. obliqua* stand and a *Pinus radiata* D. Don plantation at a distance of 0.5 km of each other. The dominant tree species in the deciduous forest is *N. obliqua*, with a subcanopy dominated by *Aextoxicon punctatum* Ruiz et Pav, and an understorey of the bamboo *Chusquea quila* Kunth and the small tree *Rhaphithamnus spinosus* (A.L.Juss) Molina. The *P. radiata* stand is a fast-growing monoculture with an understorey of *Aristotelia chilensis* (Molina) Stuntz, *Chusquea quila* and *Rubus constrictus* P.F.Müll. et Lefèvre. The *Nothofagus* stand is older (65-120 yr), has higher trees (32 m), and a lower basal area (39 m² ha⁻¹) than the pine plantation (30 yr, 24 m, 129 m² ha⁻¹, respectively).

2.1.3. Coastal mountain range

Six catchments were selected over a total area of 3,321 ha in the Coastal mountain range (39°50'-40°05' S, 73°10' -73°20'W) near Valdivia, southern Chile (Fig. 2). The climate is humid temperate. Annual rainfall increases with altitude, from about 2000 mm near the coast to approximately 6000 mm at the top of the coastal range. All catchments have relatively homogeneous physiography, geology, climate and soil. The size varies from 55 to 1462 ha, the altitude from 5-75 m to 255-700 m, and a mean slope angle from 10 to 30%. Two soil series are present in the study area; Hueycolla with a loam clay texture derived from mica schist, and Los Ulmos with deeper red clay soils derived from old volcanic ashes.

Land use cover varies between the six catchments. One catchment has second growth native forests occupying more than 92% of its surface, of which a considerable part was old-growth, and no plantations at all. Three catchments have less than 50% of their surface area converted to young (2-9 years) fast-growing

Eucalyptus plantations, and the two remaining catchments have more than 50% cover of *Eucalyptus* forest (<50 years). Shrub cover varies from 6 to 18% for the six catchments, pasture from 0 to 5%. More detailed information on the catchments is given by Oyarzún *et al.* [14].

2.2. Data collection

2.2.1. Sample collection and chemical analysis

In the four stands of San Pablo de Tregua, litterfall, bulk open field precipitation, throughfall, stemflow, soil infiltration water (10 cm depth), percolation water (>1 m), and streamflow were collected monthly from October 2002 to September 2006. During the first measuring year in San Pablo de Tregua, litterfall was separated and analyzed in different fractions (leaves, bark, reproductive organs, branches, mosses and remaining material). At Paillaco, the same fluxes were measured monthly from May 2000 to April 2001 and from June 2003 to November 2004. In the Coastal mountain range, measurements of open field precipitation and streamflow occurred from June 2003 to May 2005.

Standard field procedures were used for all measurements. Litterfall was collected using 12-15 collectors per plot that had a square collecting surface of 0.25 m² each. Aboveground water fluxes were measured using 10-15 collectors with 200 cm³ surface area funnels draining into 2 L bottles for throughfall, and with plastic collars draining into 25 L barrels around 4-6 trees for stemflow. Similar devices as for throughfall were used to collect open field precipitation. Soil infiltration water was collected with zero-tension lysimeters, percolation water with vacuum pressure lysimeters. All equipment was positioned systematically in 0.1 ha plots. Streamflow water discharge was recorded by water level recorders, and stream water samples were taken one or two times a month depending on the study site.

Leaf litter decomposition rates at San Pablo de Tregua were determined with a litterbag experiment. In each stand, 20 litterbags (20 x 20 cm² surface area, 2 mm mesh size) were filled with 20 g of oven-dried leaf litter of the stand, and installed on the forest floor in September 2006. In the evergreen pristine stands, a series of litterbags filled with *Saxegothaea conspicua* bark was installed as well. Four litterbags were collected at five time intervals over a 1 yr period of decomposition in the field.

Oven-dried litterfall fractions were analysed for total N (modified Kjeldahl method) and K⁺, Ca²⁺, and Mg²⁺ (atomic absorption spectrophotometry, AAS) after oxidation with a HNO₃ digestion. P was measured spectrophotometrically after the same digestion. Decomposed leaf litter was analyzed on N and C (elemental analyzer coupled to an isotope ratio mass spectrometer, EA-IRMS) after grinding, and on K⁺, Ca²⁺, and Mg²⁺ (AAS). All water samples were filtered (0.45 µm), electronic conductivity and pH were determined using specific electrodes, K⁺, Ca²⁺, Mg²⁺, and Na⁺ by atomic emission spectrometry, NO₃⁻-N by a colorimetric method

based on the reduction of cadmium and $\text{NH}_4^+\text{-N}$ by the phenate method. More detailed information on data collection and analysis is provided by [12-14].

2.2.2. Data analysis

Element fluxes were obtained by multiplying litterfall or water fluxes with element concentrations. Means were compared between groups using ANOVA or Kruskal-Wallis tests and t-tests or non-parametric Wilcoxon tests, depending on the validity of normality assumptions. The level of significance used was 0.05. Decomposing leaf litter mass over time was modelled using single exponential model functions.

3. Results and discussion

3.1. Litterfall and leaf litter decomposition

3.1.1. Litterfall

Total annual litterfall in the four stands in San Pablo de Tregua ranged from 3487 to 5811 $\text{kg ha}^{-1} \text{yr}^{-1}$ over the 4-year study period. These amounts are at the lower range of values (5 to 7.4 $\text{ton ha}^{-1} \text{yr}^{-1}$) reported for other *Nothofagus* forests in southern Chile [15]. No significant difference in litterfall mass was observed between the two evergreen stands. For the deciduous stands, however, mean annual litterfall was significantly lower in the managed than the unmanaged stand. This is likely due to the lower tree density and basal area in the managed stand, but may also be related to the absence of *Chusquea* bamboo litterfall there, as this understorey species was removed before tree harvesting.

With respect to the different litterfall fractions measured in 2002-2003, leaves contributed 66-81% of the total litterfall in the four stands, with an average of 73%. Similarly, the leaf litterfall contribution has been reported to range from 60 to 76% in forests worldwide [16]. In the evergreen stands, branches contributed 14%, reproductive organs 8%, and bark, mosses and remains 4%. In the deciduous stands, branch fall was relatively higher (20%), and reproductive structures (6%) and the other fractions (1%) contributed relatively less. Bark fall contributed most to litterfall (4%) in the evergreen pristine stand due to the presence of *Saxegothaea conspicua*, which periodically releases branch fragments.

The nutrient flux in the litterfall of 2002-2003 in the four stands of San Pablo de Tregua, and thus the potential return to the ecosystem, was highest for N (44-69 $\text{kg ha}^{-1} \text{yr}^{-1}$) and Ca^{2+} (39-73 $\text{kg ha}^{-1} \text{yr}^{-1}$) (Fig. 3). The K^+ flux was higher in the evergreen altered stand (25 $\text{kg ha}^{-1} \text{yr}^{-1}$) than the other three stands (4-13 $\text{kg ha}^{-1} \text{yr}^{-1}$). Furthermore, litterfall contributed 5-15 $\text{kg Mg}^{2+} \text{ha}^{-1} \text{yr}^{-1}$ and 3-4 $\text{kg P ha}^{-1} \text{yr}^{-1}$ in the four stands. In the *Nothofagus* stand at Paillaco, similar litterfall amounts and nutrient fluxes were measured as in the deciduous stands at San Pablo de Tregua. The N leaf litterfall flux in the deciduous stand at Paillaco amounted to 50 $\text{kg ha}^{-1} \text{yr}^{-1}$, with base cation fluxes of 67, 10, and 10 $\text{kg ha}^{-1} \text{yr}^{-1}$ for Ca^{2+} , K^+ , and Mg^{2+} , respectively.

3.1.2. Leaf litter decomposition

The decline in weight of decomposing leaf material in the litterbags over time could be fitted well ($r^2 > 0.88$, $p < 0.002$) using a single exponential model. The annual decomposition rate of leaf litter ranged from 0.24 to 0.47 y^{-1} for the four stands, but no significant differences in decomposition rate were found. The average decomposition rate obtained was 0.38 yr^{-1} , indicating an average mass loss of 38% after one year. The decomposition rate was significantly smaller ($p < 0.001$) for the bark litter ($k = 0.24 \pm 0.04 \text{ y}^{-1}$) in the evergreen pristine stand than for the leaf litter.

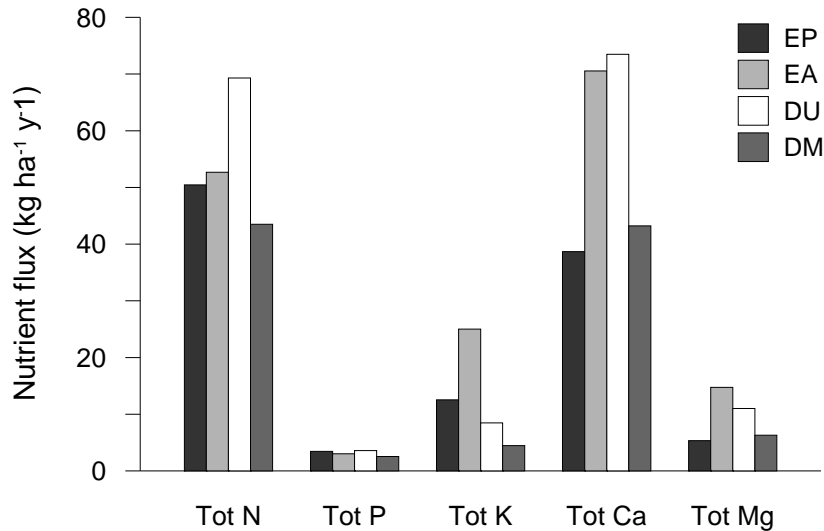


Fig. 3. Nutrient fluxes in litterfall ($\text{kg ha}^{-1} \text{ yr}^{-1}$, Oct 2002 - Sep 2003) in an evergreen pristine (EP), evergreen altered (EA), deciduous unmanaged (DU), and deciduous managed (DM) forest stand in San Pablo de Tregua, southern Chile

The nutrient dynamics in decomposing leaf litter varied between stands and nutrients. For N, no significant change in the leaf litter content was found throughout time for the evergreen pristine stand, as a result of simultaneous net mineralization and N immobilisation. For the other three stands, alternating periods of net mineralization and N accumulation were observed. For the other elements, generally a gradual decrease in nutrient content was found over time in the four leaf litter types. Often significant differences between stands were observed, but no consistent pattern appeared. Carbon dynamics over time equalled that of mass loss, and no significant differences in mass and C decomposition rates were found. The concentration of N and P in decomposing leaves increased linearly with mass loss ($r > 0.440$, $p < 0.05$). The amount of K^+ significantly declined over time, as this mobile element is readily leached from organic matter. For Ca^{2+} , significant differences in initial and decomposed leaf litter contents were observed between stands, with e.g. a much higher Ca^{2+} content in the evergreen altered stand than in the evergreen pristine stand. The Mg^{2+} amount was always significantly lower in decomposing leaves of the evergreen pristine stand than in the other three stands.

3.2. Water and dissolved nutrient fluxes

3.2.1. Precipitation, throughfall and stemflow

Over the 4-year study period at San Pablo de Tregua, on average 68 to 82% of bulk open field precipitation reached the forest floor as throughfall in the four stands, and 0.3 to 3.4% as stemflow. Throughfall water amounts were significantly higher in the managed than unmanaged deciduous stand because of the more open canopy in the former stand. Stemflow was low in the evergreen stands (< 1% of precipitation) and highest in the unmanaged deciduous stand.

In general, the nutrient flux to the forest floor by throughfall and stemflow differed significantly ($p < 0.05$) between the four stands at San Pablo de Tregua. For the deciduous stands, the dissolved nutrient input was higher in the managed than unmanaged stand, mainly because of the higher water flux in the former. For all stands, the amount of K^+ , Ca^{2+} , Na^+ , and Mg^{2+} increased when rainfall passed through the canopy due to leaching of these cations from leaves and branches and wash-off of dry deposition. For inorganic N, however, the annual flux to the forest floor by throughfall and stemflow water was significantly lower than the open field deposition at San Pablo de Tregua.

For the two forest stands at Paillaco, in contrast, the annual inorganic N flux in throughfall and stemflow ($6.5\text{--}7.5\text{ kg ha}^{-1}\text{ yr}^{-1}$) significantly exceeded the open field deposition ($2.5\text{ kg ha}^{-1}\text{ yr}^{-1}$). No significant difference in N throughfall input to the forest floor were observed between the pine plantation and the *Nothofagus* forest.

3.2.2. Canopy uptake and atmospheric deposition

Lower inorganic N fluxes below the canopy than above the canopy indicate a low atmospheric N deposition, since dry deposition of N then is lower than canopy uptake of N. Other reasons for the removal of inorganic N are conversion to gaseous N compounds, transformation to organic N, or inaccuracies in the measurements [17]. However, direct aboveground uptake of dissolved N by canopy leaves, twigs, and lichens has been demonstrated by observational and experimental studies throughout the world [3], and is the most likely explanation at San Pablo de Tregua, where significant ($p < 0.01$) linear relationships were observed between the monthly open field deposition of NO_3^- and NH_4^+ and the monthly net throughfall deposition to the forest floor. This suggests that N uptake was enhanced proportionally by an increasing N flux in open field precipitation.

At Paillaco, the difference between aboveground and belowground dissolved N fluxes allows a lower estimate of dry deposition to the forest canopy. However, this is an underestimate of the dry deposition flux because canopy uptake of inorganic N is assumed to be zero then. By taking into account canopy N uptake based on different model approaches, the dry deposition flux onto the *Nothofagus* has been

estimated at $8 \text{ kg kg N ha}^{-1} \text{ yr}^{-1}$ [13]. Comparison of the two study sites indicates that the external input of N by atmospheric deposition of inorganic N at Paillaco is clearly enhanced compared to the more pristine conditions at San Pablo de Tregua. The difference in external N input between the Paillaco and San Pablo de Tregua stands contrast with their similar internal N cycling input by litterfall (cf. 3.1.1).

3.2.3. Soil water and streamflow export

At San Pablo de Tregua, the water export below the managed deciduous stand was 11% higher than below the unmanaged stand. Nutrient concentrations in soil water infiltration, percolation, and streamflow were generally similar in both deciduous stands, except for K^+ , even though the NO_3^- concentration was significantly higher in the managed stand. As a result of higher water yield and NO_3^- concentration, mean annual NO_3^- export below the managed stand ($2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) was significantly higher than below the unmanaged stand ($1.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) during the three years after harvesting. These values are low compared to other, more industrialized regions of the world [9].

At Paillaco, a clear difference in soil water fluxes of N was found between the two adjacent studied stands. While the N flux in throughfall and stemflow was similar in both stands (cf. 3.2.1), the inorganic N flux in the soil infiltration water at 10 cm depth was significantly higher in the pine stand ($8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) than in the *Nothofagus* stand ($2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), mainly due to higher NO_3^- fluxes in the pine stand. This may be related to species-specific N uptake by tree roots, as a preference for NH_4^+ over NO_3^- has often been observed for coniferous species [18]. The higher NO_3^- concentrations in the infiltrating soil water in the pine stand suggest a profound effect of these exotic conifers on N cycling compared to the native *Nothofagus* stand. However, at 150 cm depth, N concentrations and fluxes were low and not significantly different between the two stands.

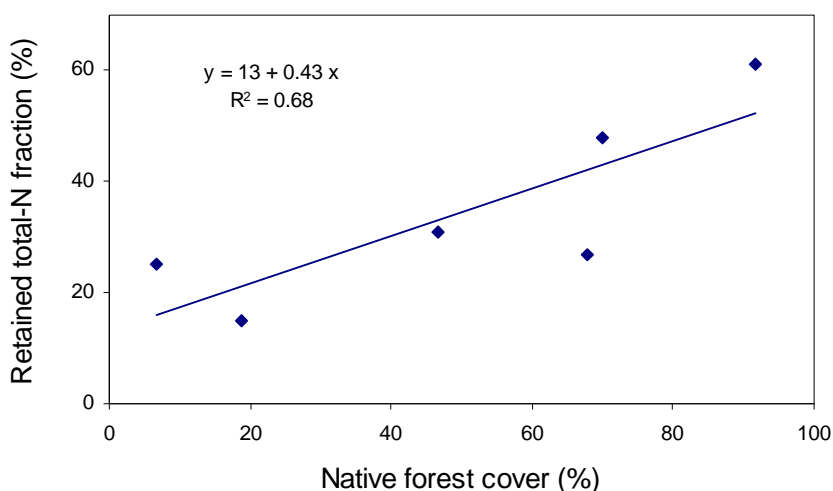


Fig. 4. Relationship between native forest cover (%) and retention (%) of total N for six catchments in the Coastal mountain range, southern Chile

For the six catchments at the Coastal mountain range, streamflux flux of inorganic N ranged from 0.3 to 2.1 kg ha⁻¹ yr⁻¹, with the contribution of NH₄⁺ generally being very low (< 0.1 kg ha⁻¹ yr⁻¹). The fluxes of water, N, and P are discussed in more detail by Oyarzún et al. [14]. Here we focus on the N export by streamflow, which was higher than the N input by open-field deposition in catchments converted to exotic species. Relative N retention increased significantly ($r = 0.83$, $p < 0.05$) with increasing native forest cover of the catchment (Fig. 4). Furthermore, the average retained total N amount was significantly higher in the catchment covered by native forest (5 kg N ha⁻¹ yr⁻¹) than in the other five catchments (0.7 - 1.9 kg N ha⁻¹ yr⁻¹) [14].

4. Conclusion

This overview of recent nutrient cycling research in temperate forest ecosystems in southern Chile focussed on two topics. First, the bilateral cooperation between Chilean and Belgian universities allowed conducting nutrient cycling research in pristine forests. The resulting baseline data on external and internal nutrient inputs to pristine forests and leaf litter decomposition rates can be important for future and current comparisons. Comparison with future similar studies will allow assessing the impact of globally changing environmental factors on nutrient cycling processes in these forests. Currently, the results demonstrate the low impact of anthropogenic derived N deposition on pristine forests in the lower Andean mountain range. Second, these studies aimed at comparing different forest types and regions. Comparison of nutrient cycling in the pristine Andean forests with stands in the central depression shows the impact of human activities such as cattle breeding on N emission and deposition to natural ecosystems. While the estimated inorganic N deposition onto forests in the central depression is still lower than in more polluted regions, the findings highlight the importance of including dry deposition estimates in forest nutrient cycling studies. Furthermore, the results of the managed and unmanaged deciduous stands indicate that native forests can be used as a wood resource with negligible disturbance of external nutrient cycling, given appropriate forest management and harvesting. Managing native forests thus could be an alternative for the ongoing conversion into exotic forest plantations in Chile. More research is needed to examine the effects of forest management and conversion on other aspects of ecosystem functioning.

Acknowledgement

The authors would like to thank Fondecyt Projects and the Bilateral Scientific and Technological Cooperation between Flanders and Chile. The first author was funded as a postdoctoral fellow of the Research Foundation - Flanders (Belgium, FWO). We acknowledge Karen Thibo, Maarten Reynaert, Nele Ameloot, Jan Vermeulen, Luc Willems, and Greet de Bruyn for their valuable contribution to the field work, sample preparation and chemical analyses.

References

- [1] S. Luyssaert, J. Staelens, and A. De Schrijver, "Does the commonly used estimator of nutrient resorption in tree foliage actually measure what it claims to?" *Oecologia* 144, 177-186, 2005.
- [2] D. Huygens, P. Boeckx, P. Templer, L. Paulino, O. Van Cleemput, C. Oyarzún, C. Müller, and R. Godoy, "Mechanisms for retention of bioavailable nitrogen in volcanic rainforest soils". *Nature Geoscience* 1, 543-548, 2008.
- [3] J.D. Sparks, "Ecological ramifications of the direct foliar uptake of nitrogen". *Oecologia* 159, 1-13, 2009.
- [4] C.E. Oyarzún, R. Godoy, A. De Schrijver, J. Staelens J., and N. Lust, "Water chemistry and nutrient budgets in an undisturbed evergreen rainforest of southern Chile". *Biogeochemistry* 71, 107-123, 2004.
- [5] J. Staelens, D. Houle, A. De Schrijver, J. Neiryneck, and K. Verheyen, "Calculating dry deposition and canopy exchange with the canopy budget model: review of assumptions and application to two deciduous forests". *Water, Air, and Soil Pollution* 191, 149-169, 2008.
- [6] N. van Breemen, "Natural organic tendency". *Nature* 415, 381-382, 2002.
- [7] J.N. Galloway, J.D. Aber, J.W. Erisman, S.P. Seitzinger, R.W. Howarth, E.B. Cowling, and B.J. Cosby, "The nitrogen cascade". *BioScience* 53, 341-356, 2003.
- [8] J.W. Erisman, and G. Draaijers, "Deposition to forests in Europe: most important factors influencing dry deposition and models used for generalisation". *Environmental Pollution* 124, 379-388, 2003.
- [9] J.A. MacDonald, N.B. Dise, E. Matzner, M. Armbruster, P. Gundersen, and M. Forsius, "Nitrogen input together with ecosystem nitrogen enrichment predict nitrate leaching from European forests". *Global Change Biology* 8, 1028-1033, 2002.
- [10] J. Aber, W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez, "Nitrogen saturation in temperate forest ecosystems - hypotheses revisited". *BioScience* 11, 921-934, 1998.
- [11] A. De Schrijver, G. Geudens, L. Augusto, J. Staelens, J. Mertens, K. Wuyts, L. Gielis, and K. Verheyen, "The effect of forest type on throughfall deposition and seepage flux: a review". *Oecologia*. 153, 663-674, 2007.
- [12] C. Oyarzún, R. Godoy, J. Staelens, C. Aracena, and J. Proschle, "Nitrogen fluxes in a *Nothofagus obliqua* forest and a *Pinus radiata* plantation in the Central Valley of southern Chile". *Gayana Botanica* 62, 88-97, 2005.
- [13] J. Staelens, R. Godoy, C. Oyarzún, K. Thibo, and K. Verheyen, "Nitrogen fluxes in throughfall and litterfall in two *Nothofagus* forests in southern Chile". *Gayana Botanica* 62, 63-71, 2005.
- [14] C. Oyarzún, C. Aracena, P. Rutherford, R. Godoy, and A. De Schrijver, "Effects of land use conversion from native forests to exotic plantations on nitrogen and phosphorus retention in catchments of southern Chile." *Water, Air and Soil Pollution* 179, 341-350, 2007.

- [15] T.T. Veblen, C. Donoso, T. Kitzberger, and J.A. Rebertus, "Ecology of southern Chilean and Argentinean *Nothofagus* forests. In: T.T. Veblen, R.S. Hill, and R.J. Read (eds.). "The ecology and biogeography of *Nothofagus* forests". Yale University Press, New Haven and London, 293-353, 1996
- [16] J.R. Bray, and E. Gorham, "Litter production in forests of the world". *Advances in Ecological Research* 2, 101-158, 1964.
- [17] J. Neiryneck, I.A. Janssens, P. Roskams, P. Quataert, P. Verschelde, and R. Ceulemans, "Nitrogen biogeochemistry of a mature Scots pine forest subjected to high nitrogen loads". *Biogeochemistry* 91, 201-222, 2008.
- [18] J. Persson, P. Gardeström, and T. Näsholm, "Uptake, metabolism and distribution of organic and inorganic nitrogen sources by *Pinus sylvestris*". *Journal of Experimental Botany* 57, 2651-2659, 2006.

Ecosystem responses of Andean *Araucaria-Nothofagus* communities after a wildfire

Leandro Paulino¹, Roberto Godoy², Pascal Boeckx³

¹Departamento de Suelos y Recursos Naturales, Universidad de Concepción, Casilla 537 Chillán, Chile, Email: lpaulino@udec.cl

²Instituto de Botánica, Universidad Austral de Chile, Casilla 567 Valdivia, Chile, Email: rgodoy@uach.cl

³Laboratory of Applied Physical Chemistry (ISOFS) UGent, Coupure links 653, B-9000 Ghent, Belgium, Email: pascal.boeckx@ugent.be

Abstract. Forest communities of *Araucaria-Nothofagus* in the Chilean Andes are adapted to wildfires. However, increases of fire frequency and severity may threaten the ecosystem. Initial responses of plant regeneration and its long term development are not well known. A conservative pattern of N fluxes could depend on the soil microbial community to adapt to the ecological processes under fire events. Enzymatic activities can be used as sensitive integrators of soil for the disturbed ecosystem. The ecological relationship of vascular plant-mycorrhiza associations may be a positive factor for recovery of the plant community. A long-term study on plant regeneration, N fluxes and ¹⁵N patterns in a soil profile, enzymatic activity and mycorrhiza relations were assessed for the first time in a severely fire disturbed *Araucaria-Nothofagus* ecosystem in Chile. The purpose was to better understand its strategy of resilience. Regeneration of some key shrubs (e.g. *Chusquea culeou*) showed an important recovery pattern of the plant community. Changes on gross N transformations and ¹⁵N patterns in the soil profile initially indicated mineral N losses into runoff water. However, the knowledge of ecosystem capacity to recover the previous patterns is not yet understood. Enzymatic activities in soil are less sensitive in this nutrient limited ecosystem and arbuscular mycorrhiza is an important way of symbiotic association with vascular plants as compared to the Northern Hemisphere. The present overview is a preliminary basis for a detailed study on the *Araucaria-Nothofagus* ecosystem resilience capacity after a severe wildfire.

1. Introduction

Forest communities of *Araucaria araucana* (Mol.) K. Koch and *Nothofagus* spp. in the Andean mountains of Chile and Argentina develop under extreme environmental conditions [1], where massive natural disturbances promote plant community dynamics. Fire is one of the alogenic disturbances that has generated discussion about dynamics of *Araucaria-Nothofagus* communities, under the current concepts of climate changes and anthropogenic activities [2,3,4,5]. However, the natural range of those Chilean plant communities correspond to climates of high precipitation during winter time and a short dry season in summer

(January to February), where the ecological and evolutionary importance of fire under a fine or broad spatio-temporal scale has been underestimated [5,6]. The floristic patterns of the southern Chile forests reflect a decreasing diversity at higher latitudes and altitudes, where the importance of herbs and shrubs increases in function of the above gradient. The importance of tree species, however, decreases.[7]. The fire effect on such patterns has not been extensively assessed and the vegetation responses to alterations should reflect the importance of some species in the north-patagonic Andes ecosystems.

In temperate forest ecosystems, nitrogen (N) is a limiting nutrient which regulates the net primary production [8]. The environment of the rainy forest ecosystems of southern Chile has been considered as a pre-industrial condition of the northern hemisphere and its current state reflects the natural processes developed during the Holocene [9,10,11]. Massive disturbances of ecosystems influence directly the dynamics of its internal processes of energy and material fluxes [4, 12, 13], where the questions related to N cycling require an analysis from a natural and anthropogenic perspective.

Soil enzymes and related parameters of microbiological activities are sensible bio-indicators of alteration impacts to the soil [14]. Several chemical reactions involve the transformation of soil organic matter and are catalyzed by enzymes which are synthesized by soil microorganisms as well as by plant roots. Simplicity and sensitivity of soil enzymatic activities to environmental changes make them a good indicator of massive changes to terrestrial ecosystems [15]. Enzymatic activity studies on nutrient transformations and short term impacts of fire to soil biochemistry come from the incipient knowledge of temperate forest ecosystems [16].

Symbiotic interactions in the soil are of great relevance, considering the importance of productive processes in forest ecosystems [17]. The advantages of mycorrhizal symbiosis to the roots of vascular plants, where the formed hyphae net allows to increase nutrient and water absorption and transport efficiency, is well known, as well as its influence on substance translocation at intra- and inter-specific levels [18]. The importance of mycorrhizal symbiosis stands out for adverse conditions of environmental stress and disturbances enhancing plant regeneration [19,20,21]. In the temperate forests of Chile, the arbuscular mycorrhiza (AM)-plant associations are more important than ectomycorrhiza which are exclusive for *Nothofagus* species [22,23,24,25]. Such ecosystems adapted to massive disturbances may be favored by this kind of symbiosis, where resistant AM spores show an important way of vegetation recovery [17].

The aim of the present research was to assess the effects of fire on vascular plant regeneration in the Tolhuaca National Park (Chile), also on N transformations and some enzymatic activities in the soil, as well as the AM colonization parameters on

the roots of *Araucaria araucana* seedlings under controlled experimental conditions.

2. Methods

The present research was made in the Tolhuaca National Park, located at the occidental slopes of the Andean mountains of Araucanía Region in Southern Chile (38° 12' S, 71° 48' W). About 60 % of the park surface was affected by a wildfire of high severity (all plants and big trees were dead in the stand) in February 2002. With the aim of assessing the fire effect on the *Araucaria-Nothofagus* forest ecosystem, permanent plots were installed in stands of severe fire (**B: burned**) and in not affected stands (**U: unburned**). The 0.1 ha (50 x 20 m down slopes) was triplicated for each site and located in slopes of south face, where vegetation, N biogeochemistry and soil microbiological studies were conducted. The study area was located at about 1,300 to 1,400 m a.s.l., with a rainy temperate climate, a high intensity of winter precipitation and about 2 dry mounts [26]. Precipitation is about 2,000 mm yr⁻¹ and average temperature of the coldest month (July) is 7.0 °C, while for the warmest month (January) it is 19.9 °C. Snowfall occurs normally between July and September, which may reach about 1 m high [27]. Soil classification is of the Andisol type and *Santa Bárbara* series, formed on recent volcanic material [28,29]. Vegetation type corresponds to forest communities with tree strata dominated by *Nothofagus spp.* and *Araucaria araucana* (Mol.) C. Koch [30,31].

Regeneration of vascular plants was studied only at the **B** area during 5 years after the fire event. On the basis of frequency, abundance and cover parameters for each species and stand, a specific value (SV) was calculated as described in [32], to assess the dynamics of plant regeneration.

The research on N biogeochemistry was done through gross mineralization/immobilization turnover analysis in the laboratory (15 months after fire), using the isotopic dilution technique as described in [33,34,35,36], with controlled incubation during 7 days. Besides, the ¹⁵N natural abundance in a detailed soil profile was evaluated during 4.5 years after the fire, as well as the mineral N (as NO₃-N) losses to runoff water in two different streams of each site. Measurements of soil mineral N was done with the colorimetric methodology of the continuous flow analysis (Skalar, Holand), where NH₄⁺-N and NO₃⁻-N were estimated as mg N kg⁻¹ dry soil [36]. Measurements of mineral N in runoff water samples were done colorimetrically with a UV/Visible spectrophotometer using a sodium nitroprussiate catalyst for NH₄⁺-N determination [37], and Cd reduction for NO₃⁻-N [38]. The ¹⁵N determinations were done by mass spectrometry (20-20, PDZ Europa, United Kingdom). Colorimetric methods were used with a UV/Visible spectrophotometer for estimation of the enzymatic activities of urease and dehydrogenase in the soil as proposed in [32]. Parameters of frequency and intensity of AM colonization on seedlings of *A. araucana* roots were measured as described in [32]. Seedlings were grown in pots under controlled conditions of the greenhouse

on different substrates as soil treatments: burned and unburned. The soils were collected from the study area sites; a control was included with an autoclaved sterilized soil (150°C during 30 min).

3. Results and discussion

The list of plant species observed during the five years of regeneration monitoring is given in Table I, according to nomenclature as described in [31].

Table I. List of species observed at the study sites in the Tolhuaca National Park, Southern Chile

Species	Family	Life form
<i>Blechnum penna-marina</i> (Poir.) Kuhn	Blechnaceae	Hemicryptophyte
<i>Lycopodium magellanicum</i> (P. Beauv.) Sw.	Lycopodiaceae	Chamaephyte
<i>Araucaria araucana</i> (Mol.) K. Koch	Araucariaceae	Megaphanerophyte
<i>Adenocaulon chilense</i> Less.	Asteraceae	Hemicryptophyte
<i>Lagenophora hirsuta</i> (Poepig ex Lesing) Dudley	Asteraceae	Hemicryptophyte
<i>Picris echioides</i> L.	Asteraceae	Hemicryptophyte
<i>Senecio pilquensis</i> Buek	Asteraceae	Hemicryptophyte
<i>Senecio vulgaris</i> L.	Asteraceae	Therophyte
<i>Sonchus</i> sp.	Asteraceae	Therophyte
<i>Berberis linearifolia</i> Phil.	Berberidaceae	Nanophanerophyte
<i>Berberis serrato-dentata</i> Lechler	Berberidaceae	Nanophanerophyte
<i>Hollermayera valdiviana</i> (Phil.) Ravenna	Brassicaceae	Hemicryptophyte
<i>Maytenus disticha</i> (Hook. f.) Urban	Celastraceae	Nanophanerophyte
<i>Maytenus magellanica</i> (Lam.) Hook. f.	Celastraceae	Megaphanerophyte
<i>Empetrum rubrum</i> Vahl ex Willd.	Empetraceae	Chamaephyte
<i>Gaultheria phillyreifolia</i> (Pers.) Sleumer	Ericaceae	Nanophanerophyte
<i>Escallonia alpina</i> Poepp. Ex D.C.	Escallonaceae	Nanophanerophyte
<i>Adesmia concinna</i> Phil.	Fabaceae	Chamaephyte
<i>Vicia nigricans</i> H. et A.	Fabaceae	Nanophanerophyte
<i>Azara lanceolata</i> Hook. f.	Flacourtiaceae	Nanophanerophyte
<i>Desmarea mutabilis</i> (P. et E.) Van Tiegh. Ex Jacks.	Loranthaceae	Nanophanerophyte
<i>Myrceugenia chrysocarpa</i> (Berg.) Kausel	Myrtaceae	Nanophanerophyte
<i>Myrceugenia parvifolia</i> (DC.) Kausel	Myrtaceae	Nanophanerophyte
<i>Nothofagus alpina</i> (P. et E.) Oerst.	Nothofagaceae	Megaphanerophyte
<i>Nothofagus antarctica</i> (G. Forster) Oerst.	Nothofagaceae	Nanophanerophyte
<i>Nothofagus dombeyi</i> (Mirb.) Oerst.	Nothofagaceae	Megaphanerophyte
<i>Nothofagus pumilio</i> (P. et E.) Krasser	Nothofagaceae	Megaphanerophyte
<i>Epilobium puerulum</i> H. et A.	Onagraceae	Hemicryptophyte
<i>Oxalis valdiviensis</i> Barn.	Oxalidaceae	Hemicryptophyte
<i>Muehlenbeckia hastulata</i> (J.E. Sm.) Johnst.	Polygonaceae	Nanophanerophyte
<i>Embothrium coccineum</i> J.R. et G. Forster	Proteaceae	Megaphanerophyte
<i>Myoschilos oblonga</i> R. et P.	Santalaceae	Nanophanerophyte
<i>Ribes magellanicum</i> Poir.	Saxifragaceae	Nanophanerophyte
<i>Solanum cyrtopodium</i> Dunal	Solanaceae	Nanophanerophyte
<i>Viola reichei</i> Skottsbo.	Violaceae	Hemicryptophyte

Table I. Continued

Species	Family	Life form
<i>Drimys andina</i> (Reiche) R.A. Rodr. & Quezada	Winteraceae	Nanophanerophyte
<i>Alstroemeria aurea</i> Graham	Amaryllidaceae	Geophyte
<i>Dioscorea brachybothrya</i> Poepp.	Dioscoreaceae	Nanophanerophyte
<i>Sisyrinchium</i> sp.	Iridaceae	Hemicryptophyte
<i>Codonorchis lessonii</i> (Brongn.) Lindl.	Orchidaceae	Geophyte
<i>Chusquea culeou</i> Desv.	Poaceae	Nanophanerophyte

The SV parameter is shown in Figure 1 for most relevant species. The importance of some nanophanerophytes, normally very resistant short shrubs, is evidenced. Among those, a very significant increasing SV was observed to *Chusquea culeou* Desv., Bambusaceae. Also for *Gaultheria phillyreifolia* (Pers.) Sleumer, Ericaceae and *Nothofagus alplina* (P. et E.) Oerst., Nothofagaceae, the last one being a macrofanerophyte (big tree) with an exclusive trunk sprout regeneration (field observations).

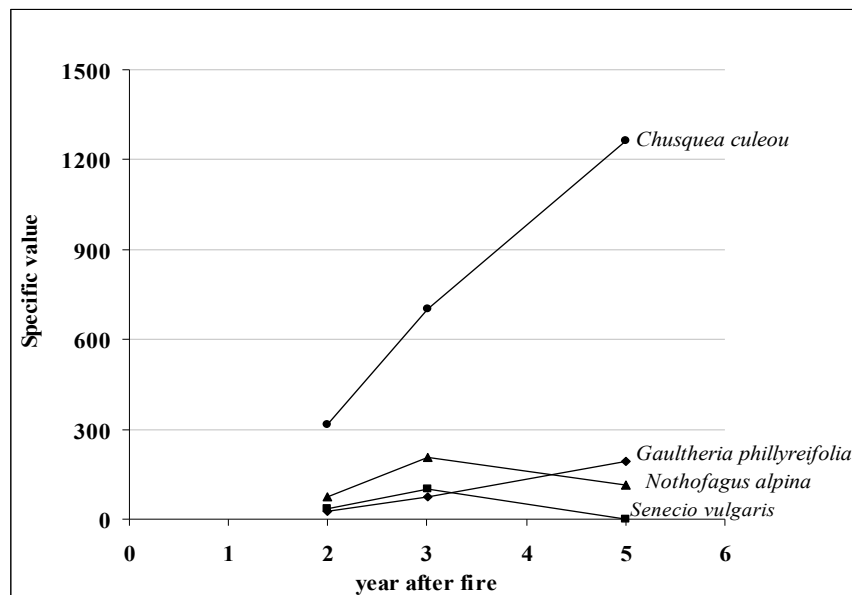


Fig. 1. Specific value (SV) of some relevant species regenerating at the burned site during five years after the fire event in the Tolhuaca National Park, Southern Chile.

The increasing high SV observed for *C. culeou* demonstrates the efficient competing capacity of the species at their niche. Seed production for *C. culeou* is very sporadic and the persistency after massive disturbances depends on their resistant rhizome [39]. The observed SV for *C. culeou* was mainly influenced by frequency and cover, compared to the abundance data (not shown), which can be interpreted as a high level of surviving corms. Although a massive plant cover disappearance after the fire, the responses of *C. culeou* recovery have not been related to light availability. Former studies have demonstrated that, in ecologically optimal communities of mixed evergreen-deciduous *Nothofagus* spp. at medium elevations in Chile, *Chusquea* spp. developed a higher value of cover as compared

to the understory of high elevation *Nothofagus pumilio* communities at the tree line where light availability is much higher [40,41].

Those patterns suggest that *Chusquea spp.* are less generalist and better competitors than other shrubs for soil nutrient resources. The community structure and site conditions are the success factors for some plant species like *Chusquea spp.*, favoring the tolerance to nutritional deficiency more than light availability [42]. These facts may explain the poor species diversity in some high elevation communities with understory dominated by *Chusquea* at advanced steps of succession [40,41]. Higher soil moisture levels have also been demonstrated as a factor of vegetation association with *Chusquea spp.* [43], which could influence significantly its regeneration in the *Araucaria-Nothofagus* communities after fire. In terms of vegetation dynamics, the non-equilibrium hypothesis has been supported to the success of *Chusquea spp.* [44], where disturbance cycles allow the initial recruitment of species as inhibitors or promoters of tree species regeneration.

In Fig. 2, the gross N transformation rates (15 months after fire) are shown of 7 days incubated soil samples. Gross ammonification (**m**) was more relevant in site **B**, mainly at the first 20 cm depth. Gross nitrification (**n**) was significantly higher at the **B** site while at the **U** site it was negligible. Ammonium immobilization (**A-i**) did not show important differences between the soil sites. However, for site **B** the ammonium consumption by microbial activity was relevant due to the high **n** flux rate. Besides, the significant nitrate immobilization (**N-i**) at site **B**, it contrasts the nitrate fluxes in site **U**.

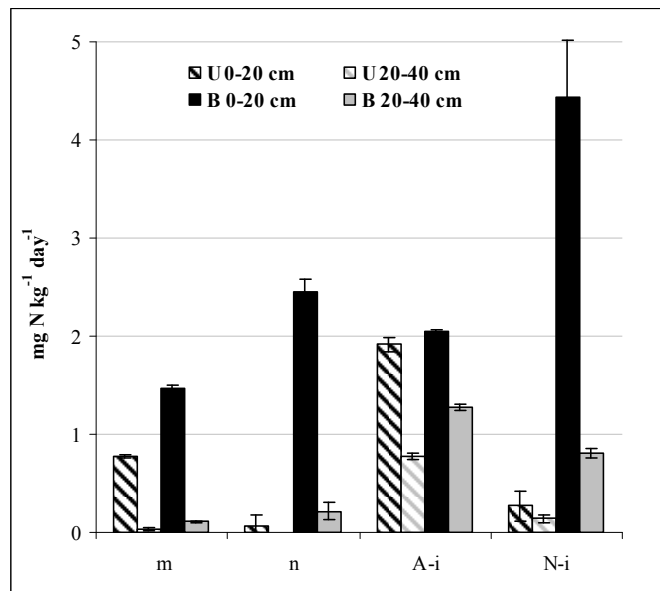


Fig. 2. Gross mineralization/immobilization rates (mg mineral N kg⁻¹ soil day⁻¹) of the burned (B) and unburned (U) soils of the Tolhuaca National Park from different depths after 7 days *ex situ* incubation; m: gross ammonification; n: gross

nitrification; A-i: gross immobilization of NH_4^+ -N; N-i: gross immobilization of NO_3^- -N

Fire activated the NO_3^- pool fluxes, which was not observed before the event (site U in Fig. 2). In conifer forest communities not affected by fire in the Northern Hemisphere a low nitrification rate has been observed in the soil profile, which was attributed to chemical inhibition of mono-terpenes [45] and phenols [46] from the litter layer on the soil. In forests of *Pinus silvestris* L., Pinaceae, of the Northern Hemisphere, adapted to fire events, a clear decrease of nitrification rates was observed in the organic profile in sites not affected by fire for a long time. This was related to an allelopathic action of exuded phenols from plant leaves of the Ericaceae family dominating the forest understory at an advanced succession step [47]. In the present study, the site U understory was dominated by *Gaultheria phyllereifolia* (Pers) Sleumer, Ericaceae (not shown) and the same floristic tendency was observed by plant regeneration dynamics (Fig. 1). The discussed mechanisms possibly regulate the N transformation processes in the soil of *Araucaria-Nothofagus* in the Andes of Chile. The low mineralization rates may indicate a strong competition between plants and soil microorganisms for labile N pools. The periodic fire events promote a release pulse of great amounts of reactive N, formally retained in the soil organic matter matrix and dead issues of litter layer.

In Fig. 3 the temporal concentration of NO_3^- -N in water samples of different streams of sites B and U is shown. After 4.5 years of fire event, a recover of the original levels of NO_3^- -N was observed in site B. However, a retrospective estimate to the fire date (area at the left side in Fig. 3) shows an exponential projection of the values ($R^2 = 0.96$), indicating a very high impact of fire on the runoff water quality. Wildfires promote NO_3^- -N leaching in the soil profile of affected forests, which is lost to streams and lakes [48]. In micro-watersheds with conifer forests in the United States, the initial effects of a prescribed fire increased NH_4^+ -N in runoff water, which quickly discontinued. However, no immediate responses on NO_3^- -N were found in the stream water, which increased about 630 times at the following years, because of an evident increase of nitrification rates in the soil profile [49].

In the present study the very significant increase of soil nitrification after fire was found to be consistent with the high concentration of NO_3^- -N in runoff water, and the initially estimated amount of N loss was comparable to the observed data in [49], with a rapid decrease over time (Fig. 3). The significant increase of gross N immobilization in the affected soil (Fig. 2) indicates an important microbial activity as a recovering ecosystem factor. After 4.5 years after the fire event the concentration of NO_3^- -N in streams of site B was the same of those in site U. However, in Northern Hemisphere ecosystems of the same patterns needed up to 15 years to recover [50]. Also, the high projection of initial N losses supports a very high capacity of resilience of *Araucaria-Nothofagus* ecosystems.

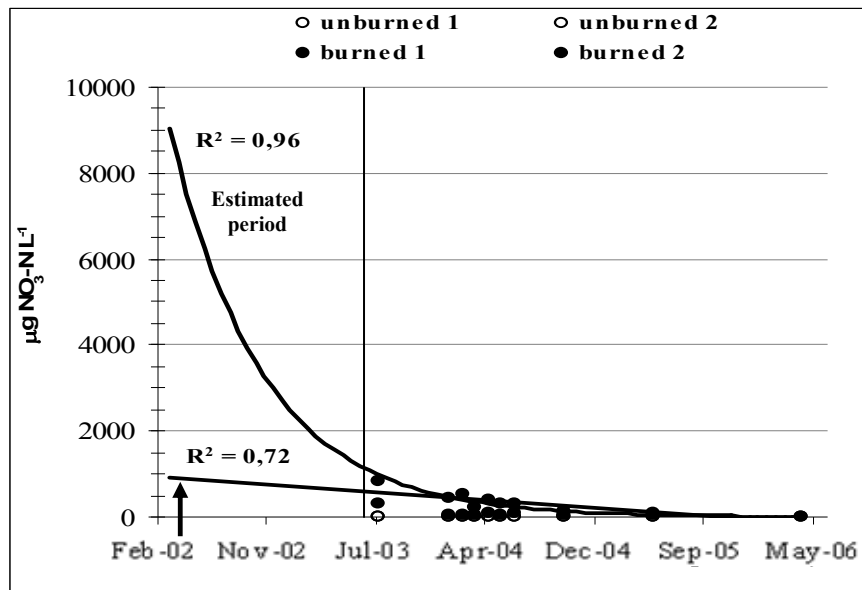


Fig. 3. Runoff water concentration of $\text{NO}_3^- \text{-N}$ ($\mu\text{g N L}^{-1}$) at different streams in the Tolhuaca National Park; the area at the left site of the vertical line corresponds to estimated projections (linear and exponential) of NO_3^- concentrations; the arrow indicates the date of fire.

In Fig. 4, the logarithmic trend of $\delta^{15}\text{N}$ in function of total N amounts in the detailed soil profiles of the studied sites is shown during different periods after the fire. The function moved up in the graph for the site **B** soil profile due to the enrichment of $\delta^{15}\text{N}$ (continuous lines) for all periods of observation, indicating no recovery to an unaffected pattern, as shown in the site **U** soil profile (discontinued lines).

The logarithmic regression of $\delta^{15}\text{N}$ in function of the total N soil pool seems to be a robust prediction model for N transformations under different environmental changes [51,52,53]. The NO_3^- losses (as immobilization, plant consumption and leaching fluxes) move the function up [51] in agreement with the $\delta^{15}\text{N}$ enrichment under a constant amount of total N, because they are high, which is consistent to the organic layer of temperate forest soils [52]. The initial deficiency to retain NO_3^- in the studied ecosystem is in agreement to the above described pattern. This interpretation has been proposed as an integrator of resilience prediction in temperate forest ecosystems after catastrophic events in Chile [53]. In the Northern Hemisphere the same patterns were previously observed and attributed to a massive loss of NO_3^- by runoff after vegetation clear cut [50].

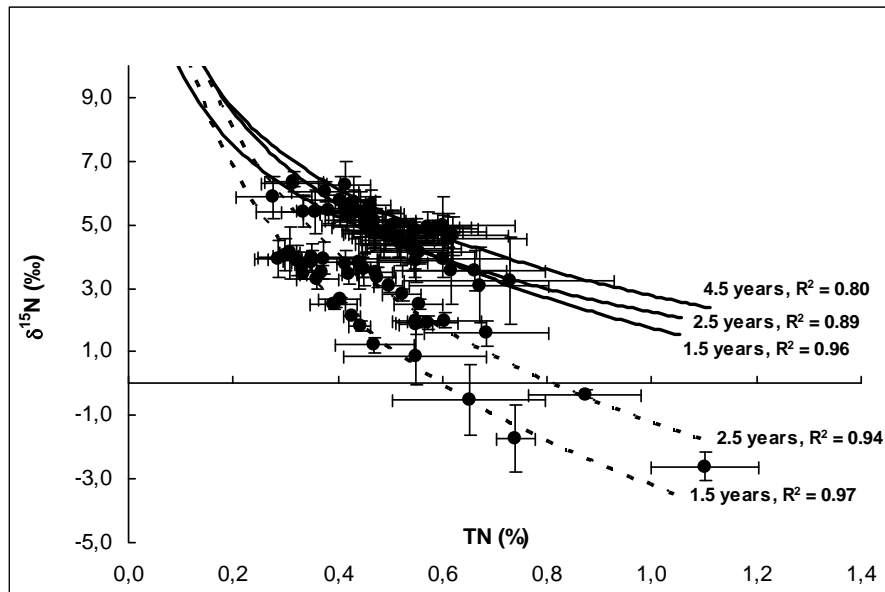


Fig 4. Logarithmic estimates of $\delta^{15}\text{N}$ ‰ in function of total soil nitrogen (TN %) for the burned (continuous lines) and unburned soil profiles (discontinued lines), after the fire event in the Tolhuaca National Park, Southern Chile.

In Fig. 5-A the average urease activity rate for three different periods (seasons) is shown. The same data can be observed in Fig 5-B for the dehydrogenase activity. At the first 20 cm depth of the soil profile, the urease activity was significantly higher in site U, with a rate of about $420 \mu\text{g N-NH}_4 \text{ g}^{-1} \text{ dry soil h}^{-1}$, while the dehydrogenase activity rate showed a double value for site U, with about $30 \mu\text{g triphenyl formazan (TPF) g}^{-1} \text{ dry soil } 48\text{h}^{-1}$. The enzymatic activity for the 20 to 40 cm depth was significantly lower than for the top soil (Fig. 5).

The importance of enzymatic activity as indicator for N mineralization related processes has been studied in *Araucaria angustifolia* forest soils [54], where the urease activity was lower than $50 \mu\text{g NH}_4^+-\text{N g}^{-1} \text{ h}^{-1}$ in a high diversity ecosystem. In a large spectrum of soil types of the Northern Hemisphere, the urease activity was about $64 (23-146) \mu\text{g NH}_4^+-\text{N g}^{-1} \text{ 2 h}^{-1}$, strongly correlated to the microbial biomass of the soil [55]. In the present research, urease activity rates far surpassed the presented literature values, suggesting a high dependence of the N limited *Araucaria-Nothofagus* ecosystem to specific enzymes for nutrient transformations. The sensitive reduction of urease activity in site B (Fig. 5) is an indication of the fire effect related to a decrease of ammonification rates (Fig. 2). A former study in volcanic soils of Chile showed a dehydrogenase activity rate of about $504 \mu\text{g TPF g}^{-1} \text{ 48 h}^{-1}$ [56]. In comparative studies of volcanic soils of Chile, a value of $176 \mu\text{g TPF g}^{-1} \text{ 24 h}^{-1}$ was observed in a red-clay soil and about $591 \mu\text{g TPF g}^{-1} \text{ 24 h}^{-1}$ in a recent volcanic (*trumao*) soil. This correlated with the amount of soil carbon [57]. These literature values surpass the observed values of dehydrogenase activity in the *Araucaria-Nothofagus* forest soils, probably because the organic matter decay is

slower in the latter environments where a high amount of recalcitrant material is available in the soil profile.

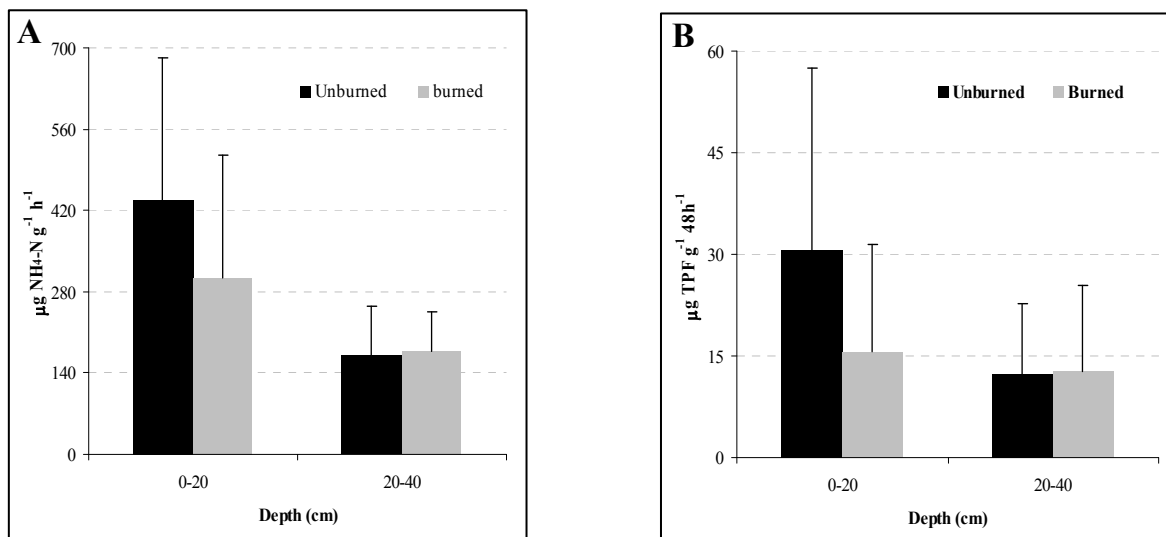


Fig 5. Enzymatic activity of **A**: urease ($\mu\text{g NH}_4^+\text{-N g}^{-1} \text{ soil h}^{-1}$) and **B**: dehydrogenase ($\mu\text{g tri-phenyl formazan g}^{-1} \text{ soil } 48 \text{ h}^{-1}$) at different depths of unburned and burned soils from the Tolhuaca National Park, Southern Chile

In Fig. 6-A, the frequency of mycorrhizal colonization in *A. araucana* seedling roots was 100% for plants growing on the **U** soil, while for those growing on the **B** site and the sterilized soil it was 73.4% and 33.8%, respectively. These differences are evident to colonization which considers also the abundance of endophytic material on roots as shown in Fig. 6-B.

The still high AM frequency colonization observed in soil **U** contrasts to former studies [23,58]. These results suggest that fire does not alter the relative presence of endophytic material from AM on plant roots, although the quantitative analysis indicates an important damage (Fig. 6-B). The present results may indicate that plant species like *A. araucana* can favorably regenerate after fire due to the resistance of mycorrhizal spores in the burned soil and survived roots. The AM species in the *Araucaria-Nothofagus* ecosystems may be well adapted to fire events and represent a relevant way of plant community recovery.

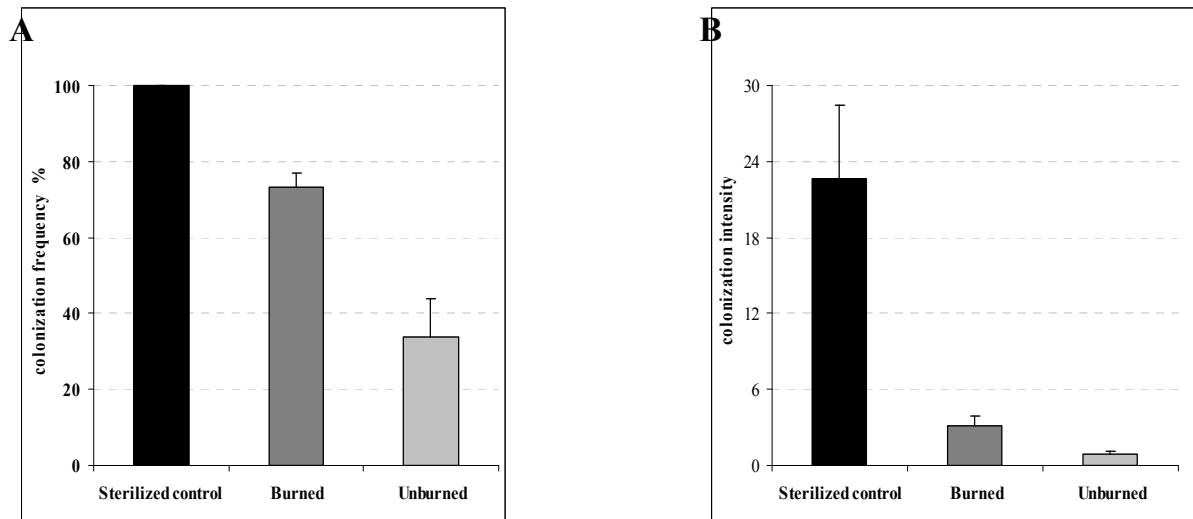


Fig.6. Colonization frequency, % (A) and intensity (B) of AM on the roots of *A. araucana* seedlings grown on different soils from the Tolhuaca National Park, Southern Chile (burned, unburned and autoclaved sterilized soils), in pots under greenhouse conditions.

4. Conclusion

The vegetation recovery in the *Araucaria-Nothofagus* forest ecosystem after a wildfire depends on key species like *C. culeou*. A long term study with multivariate parameters will elucidate functional processes not yet known. The limited N fluxes highly change with fire event however some eco-physiologic processes regulate nutrient losses and seem to be dependent of vegetation succession steps. The enzymatic activity in the soil is less sensitive than the expected but shows a consistent relation to the fire impact to the N transformations in soil. The symbiotic associations of AM-plant roots represent an important adaptation of the ecosystem to the massive disturbances of fire.

Acknowledgement

The authors would like to thank the Ministry of the Flemish Community (Project BIL “Effect of fire damage on regeneration and N loss from *Araucaria araucana* forest in Southern Chile”), and the editors for the valuable comments. L. Paulino would like to thank the *Programa Bicentenario de Ciencia y Tecnología-World Bank-UdeC*, Project (PSD-12).

References

- [1] T. Veblen, J. Armesto, R. Burns, T. Kitzberger, A. Lara, B. Leon, and K. Young, “The coniferous forests of South America” in: F. Andersson (Ed.). Coniferous forests. Ecosystems of the World Series, Elsevier, Brussels, 6, 293-317, 2005.

- [2] T. Veblen, Regeneration patterns in *Araucaria araucana* forests in Chile. *Journal of Biogeography*, 9, 11-28, 1982.
- [3] B. Burns, Fire-induced dynamics of *Araucaria araucana*-*Nothofagus antarctica* forest in the southern Andes. *Journal of Biogeography*, 20, 669-685, 1993.
- [4] T. Veblen, B. Burns, T. Kitzberger, A. Lara, and R. Villalba, "The *Ecology* of the conifers of southern South America", in N. J. Enright and R. Hill (Eds). *Ecology of southern conifers*. Melbourn University, Melbourn, 120-155, 1995.
- [5] P. Alaback, T. Veblen, C. Whitlock, A. Lara, T. Kitzberger, and R. Villalba, "Climatic and human influences on fire regimes in North and South America", in G. Bradshaw and P. Marquet (Eds.) *How landscapes change. Human disturbance and ecosystem fragmentation in the Americas*. *Ecological Studies* 162, Springer-Verlag, Berlin, 49-87, 2003.
- [6] S. Bekessy, A. Lara, M. González, M. Cortes, A. Premoli, and A. Newton, "Variación en *Araucaria araucana* (Molina) K. Koch (*Araucaria* o Pehuén)", in C. Donoso, A. Premoli, L. Gallo, and R. Ipinza (Eds.) *Variación Intraespecífica en las especies arbóreas de los bosques templados de Chile y Argentina*. Universitaria, Santiago, 215-232, 2004.
- [7] M. Arroyo, M. Riveros, A. Peñaloza, L. Cavieres, and A. Faggi, "Phytogeographic relationships and regional richness patterns of the cool temperate rainforest flora of southern South America", in R. Lawford; P. Alaback, and E. Fuentes. (Eds.) *High-latitude rainforests and associated ecosystems of the west coast of the Americas*. *Ecological Studies*, Springer, New York, 116, 134-172, 1996.
- [8] P. Vitousek, L. Hedin, P. Matson, J. Fownes, and J. Neff, "Within-system element cycles, input-output budgets, and nutrient limitation", in M. Pace, and P. Groffmann (Eds.) *Success, limitations and frontiers in ecosystems science*. Springer-Verlag, New York, 432-451, 1998.
- [9] L. Hedin, J. Armesto and A. Johnson, Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. *Ecology*, 76, 493-509, 1995.
- [10] S. Perakis and L. Hedin, Fluxes and fates of nitrogen in soil of an unpolluted old-growth temperate forest, southern Chile. *Ecology*, 82, 2245-2260, 2001.
- [11] S. Perakis and L. Hedin, Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature*, 415, 416-419, 2002.
- [12] F. Bormann, and G. Likens, "Ecosystems development and the steady state", in F. Bormann, and G. Likens (Eds.) *Pattern and process in a forested ecosystem: disturbance, development and the steady state based on the Hubber Brook Ecosystem Study*. Springer, New York, 164-191, 1981.
- [13] P. Vitousek, "Community turnover and ecosystem nutrient dynamics", in S. Pickett, and P. White (Eds.) *The Ecology of natural disturbance and patch dynamics*, Academic Press. Orlando, 325-334, 1985.
- [14] F. Schinner and R. Sonnleitner, *Bodenökologie: Microbiologie und Bodenenzymatic*. Springer Verlag, Berlin, 1996.

- [15] R. Dick, "Soil enzyme activities as integrative indicators of soil health", in C. Pankhurst; B. Doube, and V. Gupta (Eds.) *Biological and Soil Health*. Wallingford: CABI International, 1997.
- [16] T. Hernandez, C. García, and I. Reinhardt, Short-term effect of wildfire on the chemical, biochemical and microbiological properties of Mediterranean pine forest soils. *Biology and Fertility of Soils*, 25, 109-116, 1997.
- [17] S. Smith, and D. Read, *Mycorrhizal Symbiosis*. 2nd Ed. Academic Press, London, 1997.
- [18] J. Harley, The significance of mycorrhiza. *Mycological Research*, 92: 129-139, 1989.
- [19] D. Perry, and M. Amaranthus. "The plant-soil bootstrap: microorganisms and reclamation of degraded ecosystems", in J. Berger (Ed.) *Environmental restoration of the Earth*, Island Press, Washington DC, EUA, 74-102, 1990.
- [20] D. Perry, M. Amaranthus, J. Borchers, S. Borchers, S., and R. Brainerd, Bootstrapping in ecosystems. *Bioscience*, 39: 230-237, 1989.
- [21] D. Perry, T. Bell, and M. Amaranthus, "Mycorrhizal fungi in mixed-species forests and other tales of positive feedback, redundancy and stability", in M. Cannell, D. Malcolm, and P. Robertson (Eds) *The Ecology of mixed species stands of trees*. Blackwell, Oxford, 151-179, 1992.
- [22] R. Carrillo, R. Godoy, and H. Peredo, Simbiosis micorrízica en comunidades boscosas del valle central en el sur de Chile. *Bosque*, 13, 57-67, 1992.
- [23] R. Godoy, R. Romero, and R. Carrillo. Estatus micotrófico de la flora vascular en bosques de coníferas nativas del sur de Chile. *Revista Chilena de Historia Natural*, 67, 209-220, 1994.
- [24] R. Cifuentes, Asociaciones micorrízicas en los bosques del centro-sur de Chile. Tesis de Pregrado en Ingeniería Forestal. Facultad de Ciencias Forestales. Universidad Austral de Chile. Valdivia, Chile, 1995.
- [25] G. Palfner, Taxonomische studien an Ektomykorrhizen aus den *Nothofagus*-Wäldern Mittelsüdchiles. *Bibliotheca Mycologica* nr. 190, 2001.
- [26] J. Amigo, and C. Ramírez, A bioclimatic classification of Chile: woodland communities in the temperate zone. *Plant Ecology*, 136, 9-26, 1998.
- [27] A. Miller, "The climate of Chile", in W. Schwerdtfeger (Ed.) *Climates of Central and South America*. World Survey of Climatology, Elsevier. Amsterdam, 12, 113-145, 1976.
- [28] E. Besoain, "Los Suelos", in J. Tosso. (Ed.) *Suelos volcánicos de Chile*. INIA, Santiago, 26-106, 1985.
- [29] N. Stolpe, Descripciones de los principales suelos de la VIII región de Chile. Universidad de Concepción, Chillán, 2006.
- [30] C. Ramírez, Estudio florístico y vegetacional del Parque Nacional Tolhuaca (Malleco – Chile). Museo Nacional de Historia Natural, Publicación Ocasional, 24, 3-23, 1978.
- [31] W. Pollmann, Caracterización florística y posición sintaxonómica de los bosques caducifolios de *Nothofagus alpina* (Poepp. et Endl.) Oerst. en el centro-sur de Chile. *Phytocoenologia*, 31, 353-400, 2001.

- [32] L. Steubing, R. Godoy, and M. Alberdi, Métodos de ecología vegetal. Monografías. Universitaria. Santiago, 2002.
- [33] R. Hauck, Nitrogen isotope radio analysis, in A. Page, R. Miller, and D. Keeney (Eds.) Methods of soil analysis. Soil Science Society of America, Medison, 735-779, 1982.
- [34] N. Saghir, R. Mulvaney and F. Azam, Determination of nitrogen in microdiffusion in mason jars. 1. Inorganic nitrogen in soils extracts. Communications in Soil Science and Plant Analysis, 24, 1745-1762, 1993.
- [35] R. Stevens, and R. Laughlin, Determining nitrogen-15 in nitrite or nitrate by production nitrous oxide. Soil Science Society of America Journal, 58, 1108-1116, 1994.
- [36] F. Accoe, P. Boeckx, G. Busschaert, O. Hofman, and O. Van Cleemput, Gross N transformation rates and net N mineralization rates related to the C and N contents of soil organic matter fractions in grassland soils of different age. Soil Biology and Biochemistry, 36, 2075-2087, 2004.
- [37] F. Koroleff, Determination of total nitrogen in natural seawaters by means of persulfate oxidation. International Council for the Exploration of the Sea (ICES). Pap. C.M., 1970.
- [38] D. Keeney, and D. Nelson, "Nitrogen-inorganic forms", in A. Page; R. Miller and D. Keeney (Eds.). Methods of analysis, Part 2. ASA and SSSA, Madison, Agronomy 9: 643-698., WI, EEUU, 1982.
- [39] C. Donoso, Bosques templados de Chile y Argentina. Variación, Estructura y Dinámica. Editorial Universitaria, Santiago, 1998.
- [40] T. Veblen, D. Ashton, F. Schlegel, and A. Veblen, Distribution and dominance of species in the understorey of a mixed evergreen-deciduous *Nothofagus* forest in south-central Chile. Journal of Ecology, 65, 815-830, 1977.
- [41] T. Veblen, A. Veblen, and F. Schlegel, Understorey patters in mixed evergreen-deciduous *Nothofagus* forests in Chile. Journal of Ecology, 67, 809-823, 1979.
- [42] P. Donoso, Estructure and growth in coastal evergreen forests as the bases for uneven-aged silviculture in Chile. PhD Thesis, College of Environmental Science and Forestry, State University of New York, Syracuse, 208-215, 2002.
- [43] C. Ramírez, H. Figueroa, L. Carrillo, and F. Contreras, Estudio fitosociológico de los estratos inferiores en un bosque de pino (Valdivia, Chile). Bosque, 5, 65-81, 1984.
- [44] T. Veblen, Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. Bulletin of the Torrey Botanical Club, 109, 474-487, 1982.
- [45] L. Paavolainen, V. Kitunen, and A. Smolander, Inhibition of nitrification in forest soil by monoterpenes. Plant and Soil, 205, 147-154, 1998.
- [46] T. Deluca, M. Nilsson, and O. Zackrisson, Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. Ecologia 133, 206-214, 2002.
- [47] D. Wardle, O. Zackrisson, G. Hörnberg, and C. Gallet, The influence of island area on ecosystem properties. Science, 277, 1296-1299, 1997.

- [48] J. Knoepp, and W. Swank, Comparison of available soil nitrogen assays in control and burned forested sites. *Proceedings of the Soil Science Society of America*, 59, 1750-1754, 1995.
- [49] W. Covington, and S. Sackett, Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *Forest Ecology and Manegement*, 54, 175-191, 1992.
- [50] L. Pardo, F. Hemond, J. Montoya, T. Fahey, and T. Siccama, Response of the natural abundance of ^{15}N in forest soils and foliage to high nitrate loss following clear-cutting. *Canadian Journal of Forest Research*, 32, 1126-1136, 2002.
- [51] F. Buzek, J. Cerny, and T. Paces, The behaviour of nitrogen isotopes in acidified forest soils in the Czech Republic. *Water, Air, and Soil Pollution*, 105, 155-164, 1998.
- [52] H. Vervaet, Interaction between ecosystems: the influence of intensive agriculture on NH_x deposition and N transformation processes in forest soils. Ph.D. Thesis in Applied Biological Scieces. Ghent University, Belgium, 1-213, 2003.
- [53] P. Boeckx, L. Paulino, C. Oyarzún, O. Van Cleemput and R. Godoy, Soil $\delta^{15}\text{N}$ patterns in old-growth forests of southern Chile as integrator for N-cycling. *Isotopes in Environmental and Health Studies*, 41, 249-259, 2005.
- [54] F. Carvalho, Atributos bioquímicos como indicadores da qualidade de solo em florestas de *Araucaria angustifolia* (Bert.) O. Ktze. no Estado de São Paulo. Dissertação de Mestrado em Ecologia de Agroecossistemas, Universidade de São Paulo, 2005.
- [55] S. Klose, and M. Tabatabai, Urease activity of microbial biomass in soils. *Soil Biology and Biochemistry*, 31, 205-211, 1999.
- [56] G. Ojeda, Determinación de la actividad biológica en suelos volcánicos por medio de mediciones enzimáticas y de ATP. Tesis Bioquímica. Universidad Austral de Chile, 1996.
- [57] D. Frank, *Umweltauswirkungen des Landnutzungswandels in der IX region Chiles*. Mensch Buch Verlag, Germany, 1998.
- [58] R. Godoy, and R. Mayr, Caracterización morfológica de micorrizas vesículo-arbusculares en coníferas endémicas del sur de Chile. *Bosque*, 10, 89-98, 1989.

Effect of wildfire on soil organic matter in an Andisol of a southern Chilean temperate rain forest

Yessica Rivas¹, Roberto Godoy¹, Dries Huygens², Pascal Boeckx³,
Francisco Matus⁴, Heike Knicker⁵

¹ Instituto de Botánica, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: andreatisnao@gmail.com, rgodoy@uach.cl

² Instituto de Ingeniería Agraria y Suelos, Universidad Austral de Chile, Casilla 567,
Valdivia, Chile, Email: dries.huygens@ugent.be

³ Laboratory of Applied Physical Chemistry-ISOFYS, Ghent University, Coupure links
653, B-9000 Ghent, Belgium, Email: Pascal.Boeckx@Ugent.be

⁴ Departamento de Ciencias Químicas, Universidad de La Frontera, Casilla 54-D,
Temuco-Chile, Email: fmatus@ufro.cl

⁵ Lehrstuhl für Bodenkunde, TU München, D-85350 Freising, Weihenstephan, Germany,
Email: knicker@irmase.csic.es

Abstract. Old-growth forests of southern Chile represent an important reserve of temperate forests worldwide. The precipitation chemistry in Chile still reflects the time of pre-industrial conditions. Thus, the productivity of the ecosystem mainly depends on the internal cycling of soil organic matter (SOM). However, catastrophic events, such as wildfires can initiate important changes in the physical and biogeochemical properties of SOM and therefore on the ecosystem habitat. We studied *Araucaria-Nothofagus* forests in the Andean mountains of Chile (38° S, 71° W) three years after they were affected by a huge wildfire in February 2002. The aims of this investigation were: (1) to analyze the effect of fire on the quality of SOM at different soil depths and (2) the changes in carbon content of an incomplete combustion of vegetal material after wildfire, refractory to decomposition, referred to as black carbon (BC). We used a combination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses and SOM fractionation. The chemical and elemental composition of the soil samples was studied by solid state ^{13}C CPMAS NMR spectroscopy and BC determination. We found an increase in nitrification rates after fire, and a wider aromatic C to alkyl C ratio of the incorporated char, leading to an increase in BC quantity. Our results point out that wildfire induces changes in the chemical composition of the SOM. A clear relationship between isotopic SOM signature and C and N cycling processes could be established. This indicates that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and NMR techniques can be used as proxy to assess the fire impact on the SOM dynamics.

1. Introduction

The southern cone of America represents an important reserve of worldwide temperate pristine forests [1]. Significant parts of these unpolluted forest reserves are dominated by the conifer *Araucaria araucana* (Mol.) K. Koch., in association

with several species of genus *Nothofagus* [2]. This area represents a remnant of the *A. araucana* original distribution [2, 3]. Fire is the most important disturbing effect that fragmented the *Araucaria-Nothofagus* forests of South-Central Chile and Argentina [4,5]. Fire disturbances may alter the SOM turnover and related soil characteristics [2,6] As such, incorporation of charred plant residues into the soil is expected to increase the passive SOM pool [7,8]. Postfire nitrification has been previously noted to cause a strong increase in soil NO_3^- , and because nitrification discriminates against ^{15}N , this may in turn lead to a ^{15}N -enriched residual total N pool over the time [9,10]. On the other hand, the high percentage of the lighter N (^{14}N) was lost relative to the heavier N (^{15}N), indicating that the lighter isotope is preferentially volatilized, leaving compounds that are already isotopically enriched [10]. Studies of fire effects on $\delta^{13}\text{C}$ in soils have primarily focused on changes in soil $\delta^{13}\text{C}$ because of quality vegetation changes due to fire [11] and the changes in soil C isotopic composition due to aromatic C of the incorporated char into the soil too [12]. The goals of this study were, three years after the catastrophic event, (1) to analyze the effect of the fire on the quality of SOM at different soil depths, (2) to quantify changes in “Black Carbon” (BC) content after wildfire, and (3) to evaluate the impact of fire on the chemical composition of SOM. We expected that fire involves the selective preservation of depleted C compounds (lignin and other aromatic ring compounds, etc.) during chemical changes in SOM composition. On the other hand, we expect that fire stimulates the autotrophic nitrification process, resulting in the enrichment of ^{15}N depleted NO_3^- compounds. We hypothesize that fire would result in the depletion of ^{13}C and enrichment of ^{15}N in the SOM.

2. Materials and methods

2.1 Site description and soil sampling

Forest vegetation is characterized as an *Araucaria araucana* (Mol) K. Koch - *Nothofagus spp* (*Araucaria-Nothofagus*) forest ecosystem in the Tolhuaca National Park (38°10' to 38°15' S, 71°41' to 71°50' W, 1100-1300 m a.s.l.) in the Andean mountains of southern Chile. More than half of the National park area (ca. 20,000 ha) was affected by wildfire in February 2002 [13]. Precipitation is surpassing 2,500 mm yr⁻¹. The climate is temperate -cold. The average temperature is 7.0°C in the coldest month (July) and 19.9°C in the warmest month (January) [14]. Snowfall events occur usually between July and September [15]. The soil is an Andisol according to the USDA classification [16].

2.2 Experimental design

Unburned (UB) and burned (B) study sites were selected in two comparative forest areas, dominated by *Araucaria araucana* and *Nothofagus spp*. The selected stands possessed a similar slope, aspect, altitude and soil depth. Both sites are at 1 km apart from each other. Soil samples were taken from three plots in UB and B at a

depth of 0 - 5, 5-10, 10-20 and 20-30 cm in three independent soil pedons. Thus, in total 24 soil samples were taken for analysis three years after the catastrophic event.

2.3 Analyses of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, total C (TC) and total N (TN) in the whole soil

The isotopic and elemental C and N analyses were performed using an elemental analyser (ANCA-SL, PDZ-Europe, UK) coupled to an Isotope Ratio Mass Spectrometer (20-20, SerCon, UK). The measured isotopic ratios are expressed as δ values (‰) relative to Vienna Pee Dee Belemnite (VPDB), and atmospheric air for ^{13}C for ^{15}N , respectively. The working standard was flour with a $\delta^{13}\text{C}$ value of $-27.01 \pm 0.04\text{‰}$, a TC content of $39.95 \pm 0.40\text{‰}$, a $\delta^{15}\text{N}$ value of $2.69 \pm 0.15\text{‰}$ and a total N content of $1.75 \pm 0.04\text{‰}$ (both certified by the Iso - Analytical, UK).

2.4 Chemical composition of SOM

The material remaining after oxidation with diluted potassium dichromate, referred to as resistant elemental carbon (OREC), was regarded as black carbon (BC) [7]. Briefly, between 250 and 400 mg hydrofluoric acid (HF) treated soil was oxidized with 40 ml of 0.1 M $\text{K}_2\text{Cr}_2\text{O}_7$ and 2 M H_2SO_4 solution at 60°C in an ultrasonic bath [12]. The samples were treated for 6 hours. For all samples, the oxidation was performed in duplicate and the C- and N-losses of the soil samples were calculated relative to the HF-treated samples in a carbon balance. Thereafter, HF mineral-free samples were analyzed by solid-state ^{13}C NMR spectra of on a Bruker DSX-200 NMR spectrometer. The chemical shift regions 0–45, 45–110, 110–140, 140–160 and 160–220 ppm were respectively: alkyl C, O-alkyl C, C substituted aryl C, O substituted aryl C and carboxylic C [17, 18].

2.5 Potential N mineralization

An incubation experiment was conducted to examine the potential N mineralization. First, air dried bulk soil samples from the four depth layers were brought to gravimetric water content, corresponding to 60% water-filled pore space, calculated with the bulk density of intact soil cores taken from the field. Three replicates of 30 g air dried soil were incubated in a 0.25 L plastic flask. The flasks were covered with parafilm to permit gas exchange, while retard water loss. The incubation was conducted in a growth chamber with a constant temperature of 15°C . Sampling was performed at day 0, 3, 5, 7 and 15; extraction was done with a 1:2 soil: extracting KCL (1M) solution for $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ determination, using a continuous flow autoanalyzer (Bran and Luebbe, Germany).

2.6 Statistical analysis

Statistical analysis was done using Statistics 6.0 software. For each sampling depth, an analysis of variance (ANOVA) was conducted to determine the effect of wildfire. The mean separation of ANOVA results was determined using Turkey's post-hoc test ($P < 0.05$).

3. Results

3.1. CT, NT, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and chemical shift of whole soil in the profile

There were no significant differences in CT (g C kg^{-1} soil) and NT (g N kg^{-1} soil) at different soil depths. The $\delta^{13}\text{C}$ values varied between -24.9 and -25.5‰ in unburned soil and from -26.0 to -26.7‰ in burned soil; at the different soil depths no significant differences in $\delta^{13}\text{C}$ values were found. The $\delta^{15}\text{N}$ varied of 5.71 to 0.8‰ in unburned soil, and from 6.3 to 2.8‰ in burned soil. Significant differences in $\delta^{15}\text{N}$ values were found in all soil profiles with exception for the 10-20 cm depth.

The chemical shift of HF treated soil samples and OREC samples are shown in Fig. 1a and 1b. The control soil (Fig. 1) shows a high signal assigned to alkyl C (~ 74%). The dominant peak in this region at 31 ppm is generally assigned to lipids, cutin, suberin, waxes and other aliphatic biomacromolecules [12, 19]. However, burned soil (Fig.2) shows a relative increase of the signal assigned to aryl-C (110-160 ppm). The dominant peak in this region at 135 ppm is generally assigned to aromatic C–O and C–N of lignin, black carbon and other aromatic compounds [12, 19]. The black carbon content expressed as OREC, almost does not exist in the unburned control soil. However, burned soils presented the highest contribution of aryl C, mainly for the top 5 cm depth (Fig. 2 and 3).

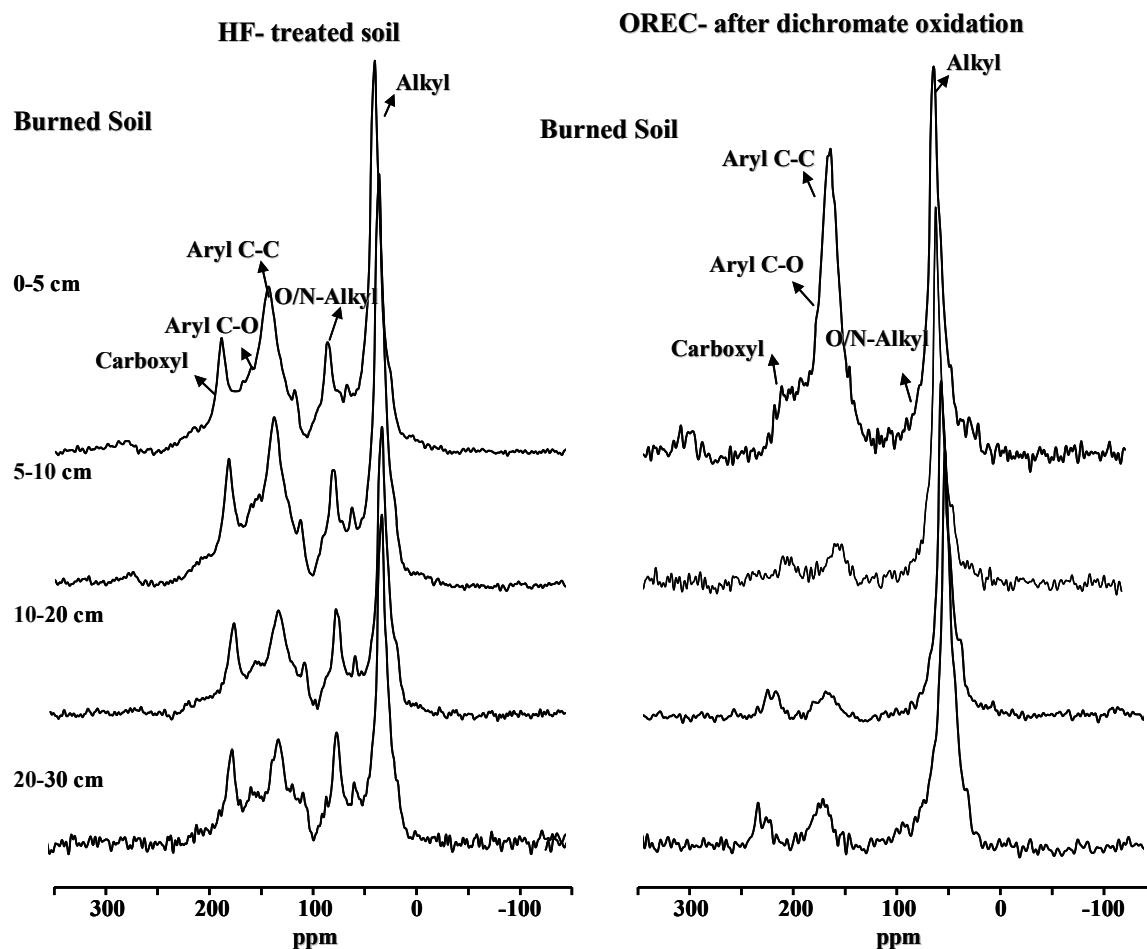


Fig. 1. Solid-state ^{13}C NMR spectra of the residue after HF treatment and after dichromate oxidation (OREC) for the unburned *Araucaria-Nothofagus* forest ecosystem in the Tolhuaca National Park, Southern Chile.

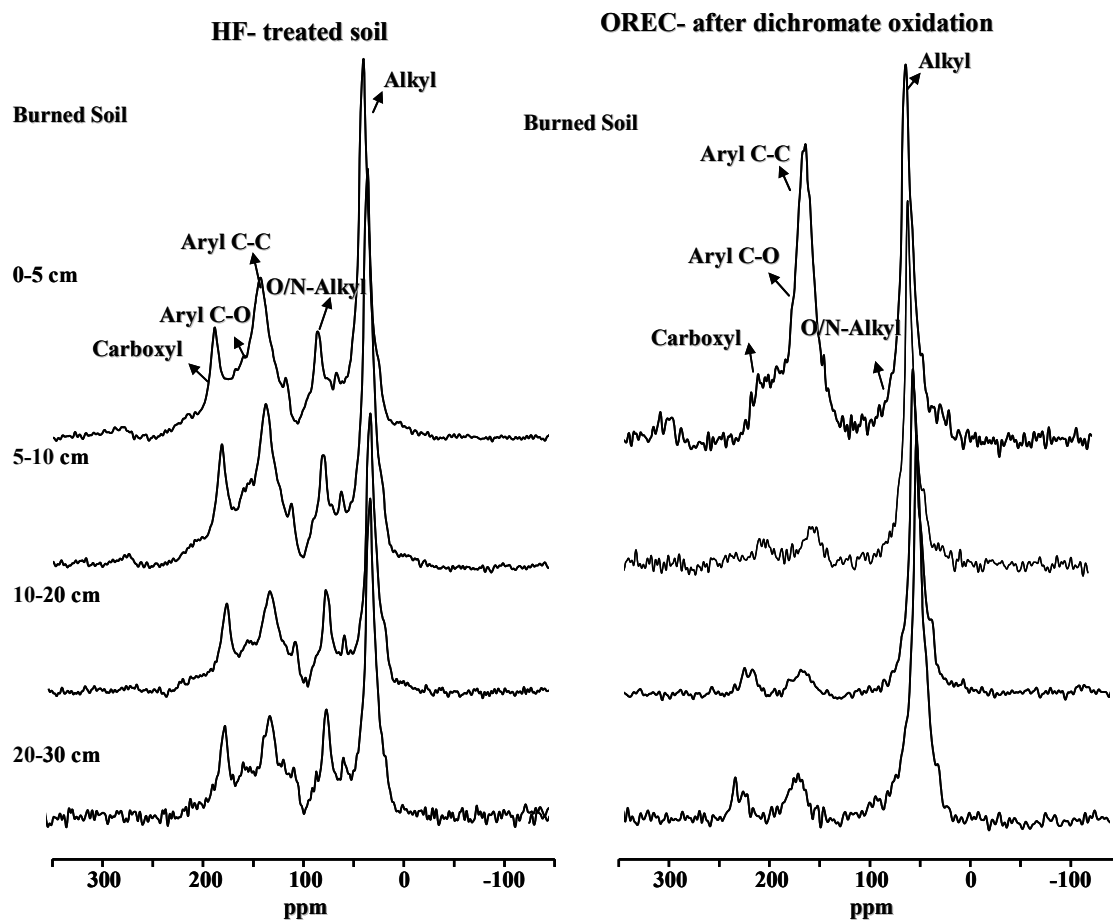


Fig. 2. Solid-state ^{13}C NMR spectra of the residue after HF treatment and after dichromate oxidation (OREC) for the burned *Araucaria-Nothofagus* forest ecosystem in the Tolhuaca National Park, Southern Chile.

We found a positive and significant correlation between $\delta^{13}\text{C}$ stable isotope values in the whole soil and the aryl-C ($r^2 = 0.65$) (Fig. 4). However, no correlation was found between $\delta^{15}\text{N}$ and aryl-C.

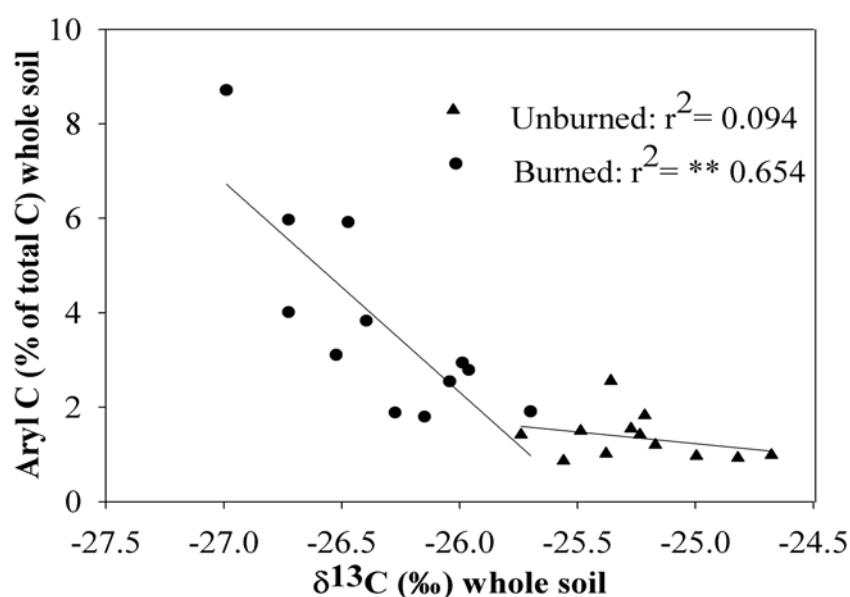


Fig. 3. Relationship between aryl-C (% of total carbon) and $\delta^{13}\text{C}$ (‰) of the whole soil for different soil depths for the unburned and the burned *Araucaria-Nothofagus* forest ecosystems in the Tolhuaca National Park, Southern Chile.

3.2. Quantitative contribution of BC

The BC (OREC) as a % of initial C content is presented in Fig. 4. The oxidation residues of burned soil ranged from 12% to 5%. The control area presented the lower values and ranged from 6% to 7%, being homogeneous for all soil depths. A higher percentage was found until 10-20 cm; thereafter, the values were uniform.

3.3 Net potential N mineralization rates

Net potential ammonification, after incubation of soils from different depths, ranged from -1.1 to 1.7 mg $\text{NH}_4^+\text{-N kg}^{-1}$ soil for the unburned soil, and from -0.5 to 0.7 mg $\text{NH}_4^+\text{-N kg}^{-1}$ soil for the burned soil. ANOVA revealed no effect of fire. The net potential nitrification varied between 2.0 to -0.7 mg $\text{NO}_3^-\text{-N kg}^{-1}$ soil for the unburned soil and between 14.1 to -1.2 mg $\text{NO}_3^-\text{-N kg}^{-1}$ soil for the burned soil. Net potential ammonification and nitrification rates are shown in Table I. Ammonification rates ranged from 1.32 to 0.60 mg $\text{NH}_4^+\text{-N kg}^{-1}$ soil d^{-1} for the unburned soil and between -0.66 to 0.54 mg $\text{NH}_4^+\text{-N kg}^{-1}$ soil d^{-1} for the burned soil. On the other hand, the nitrification rate ranged from -1.1 to 0.31 mg $\text{NO}_3^-\text{-N kg}^{-1}$ soil d^{-1} for the unburned soil and from -3.83 to -2.59 mg $\text{NO}_3^-\text{-N kg}^{-1}$ soil d^{-1} for the burned soil. However, we did not find a significant difference between the plots in the studied area, due to high standard deviations found for each sample.

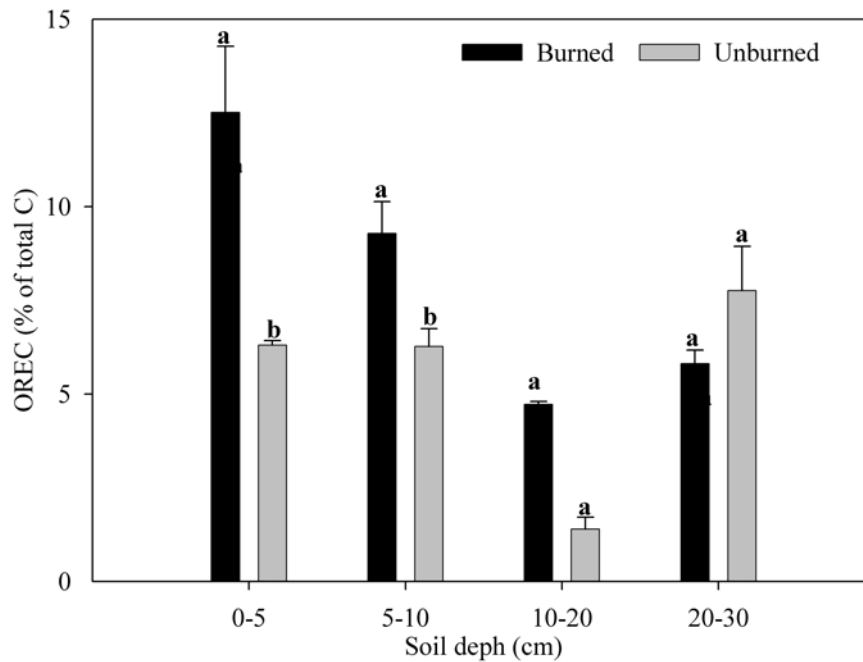


Fig. 4. Black Carbon as oxidation resistant elemental C (OREC) at different soil depths for unburned and burned soils from the *Araucaria-Nothofagus* forest ecosystems in the Tolhuaca National Park, Southern Chile

Table I. Potential mineralization rate in soil layers of unburned and burned *Araucaria-Nothofagus* stands; standard deviations are between brackets; significant differences ($P < 0.05$) between treatments in the same soil layers are indicated by different letters

Depth (cm)	N mineralization rate (mg NH ₄ ⁺ -N kg ⁻¹ d ⁻¹)		Nitrification rate (mg NO ₃ ⁻ -N kg ⁻¹ d ⁻¹)	
	Unburned	Burned	Unburned	Burned
0-5	1.32± 0.29 ^a	0.54 ± 0.20 ^a	0.01 ± 0.01 ^a	-3.83 ± 2.77 ^a
5-10	1.44± 0.06 ^a	0.52 ± 0.01 ^a	-1.10 ± 0.12 ^a	-3.76± 2.10 ^a
10-20	0.69± 0.04 ^a	-0.66 ± 1.36 ^a	-0.33 ± 0.11 ^a	-2.33± 2.66 ^a
20-30	0.60± 0.19 ^a	0.43 ± 0.37 ^a	0.31 ± 0.04 ^a	-2.59± 2.83 ^a

4. Discussion

Several studies indicate that wildfires are the most important disturbance factor in pristine forests [20,21,22]. Chemical soil properties have a direct effect on biomass productivity and SOM dynamics. Thus, alteration during fire can substantially affect SOM quality and quantity, both in the short and long term [20, 19].

Whole soil was depleted in $\delta^{13}\text{C}$ and enriched in $\delta^{15}\text{N}$ in burned sites, while unburned soil had an opposite behaviour. Changes in isotopic nutrient composition between both sites can be explained by losses and transformations of SOM compounds [10]. Losses of labile material due to fire generate a residual SOM containing more recalcitrant C compounds such as lignin and charcoal [23,20]. Easily lost compounds, such as cellulose and hemicellulose are typically enriched in $\delta^{13}\text{C}$ by 1-2‰ relative to whole plant material. Moreover, aromatic aminoacids, phenylalanine and tyrosine, being principal precursors of lignin, are relatively depleted in ^{13}C [24]. Lignin is $\delta^{13}\text{C}$ depleted by 2-6‰ relative to whole plant material [25]. Another reason why burned soil is more depleted in $\delta^{13}\text{C}$ can be the incorporation of BC because of fire [25]. We compared the chemical shift regions of ^{13}C CPMAS NMR and found a higher percentage of aryl-C (assigned to aromatic C–C and C–H of lignin, charcoal and other aromatic compounds) in the burned soil as compared with the unburned soil. Similar results were pointed out by Murage *et al.* [26], who found that charcoal, equivalent to our BC samples were depleted in ^{13}C relative to whole soil. Rumpel *et al.* [12] found that fresh black carbon with relative values of $\delta^{13}\text{C}$ of 29.2‰, which may indicate that fire can contribute to conservation of aryl-C (aromatic C, lignin, black carbon and other aromatic compounds), components that are depleted in ^{13}C . However, there was no correlation between $\delta^{15}\text{N}$, stable isotope in the whole soil and aryl-C. Therefore, the enrichment in $\delta^{15}\text{N}$ in the soil found three years after the fire is due to enhanced nitrification rates. That has its origin in the increased charcoal material due to fire. Therefore, wildfire strongly modifies the composition of soil organic N forms, reducing the most labile fractions and enhancing the most recalcitrant pools [27,28]. So, post-fire nitrification was increased by the autotrophic process in which $\text{NH}_4^+\text{-N}$ is converted to $\text{NO}_3^-\text{-N}$ [29]. Post-fire studies on N pools in the same ecosystems showed a 2 to 26 fold increase in the soil ammonium ($\text{NH}_4^+\text{-N}$) in the first year of measurements, while in this study we found a 3- to 4-fold increase in soil nitrate concentration after three years post-fire. The excess of nitrate enriched the soil and plant in $\delta^{15}\text{N}$. Similar results after wildfire was observed by Boeckx *et al.* [30] in a site very near to our study area. The same behaviour was found by Montaldo [3], but also opposite trends were reported by Covington and Sackett [32].

According to DeLuca *et al.* [29], higher nitrification rates in burned soils might be related to the increased abundance of charcoal in burned soils. Otherwise, charcoal has the potential to enhance nitrification due to increased fixed N and improved availability of other nutrients (B, Mo, K, Ca and P), as well as a higher pH. In addition, charcoal has the capacity to adsorb organic components [33] that might induce NO_3^- immobilization or sorb compounds that are otherwise inhibitory to nitrification [34]. Similar results were discussed by DeLuca *et al.* [29], who found a higher nitrate concentration in the presence of charcoal as compared to unburned soil. In our study, NH_4^+ immobilization decreased as a result of burning (data not showed). Lower N mineralization rates might be expected if microbial biomass is substantially reduced afterwards. DeLuca *et al.* [29] and Yamato *et al.* [37] showed that biochar itself contained small amounts of nutrients that would be

available to both soil biota (including mycorrhizal fungi) and plant roots. Lastly, DeLuca *et al.* [29] showed that biochar from forest wildfire stimulated net nitrification rates, most likely by adsorbed inhibitory phenols. On the other hand, according to Rondon *et al.* [38] and Warnock *et al.* [39] mycorrhizal infection increases when biochar was added to soil.

5. Conclusions

Our results with respect to C dynamics suggest that fire induces changes in C composition of the SOM, towards more depleted C compounds due to more charcoal components which are involved in selective preservation of aromatic rings originating from lignin. This results in less ^{13}C in the residue left behind in aromatic-rich char. With respect to N dynamics, we found increased nitrification rates after fire and because nitrification discriminates against ^{15}N , this may in turn lead to a ^{15}N -enriched residue in the soil. This conclusion indicates that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ can be used as proxy to assess the effect of fire on C and N dynamics. This conclusion is valid, especially for the upper soil layer (0-10 cm).

Acknowledgements

The authors would like to thank the Fondecyt Projects 1085081, the Bilateral Scientific and Technological Cooperation between Flanders and Chile, Mecesusup (UCO-UACH), PhD Scholarship by CONICYT, Dirección de Investigación Universidad Austral de Chile (DID-UACH), the staffs from ISOFYS, Gent, Belgium and the Soil Lab München, Freising, Germany. The authors would like to thank the Prof. Dr. Oswald Van Cleemput for his valuable comments on early version of this paper.

References

- [1] S. A. Bekessy, M. Lara, M. González, M. Cortés, L. Gallo A. C. Premoli, and A.C. Newton, Variación en *Araucaria araucana* (Molina) K. Koch (Araucaria o Pehuén). pp. 277-297. In C. Donoso et al. (ed). Variación Intraespecífica en las especies arbóreas de los bosques templados de Chile y Argentina. Editorial Universitaria. Santiago de Chile, 2004.
- [2] T. Veblen, Regeneration patterns in *Araucaria araucana* forests in Chile Journal of Biogeography, 9, 11-28, 1982.
- [3] P. Montaldo, La bioecología de *Araucaria araucana* (Mol) Koc. Instituto Forestal Americano de Investigación y Capacitación, Boletín N° 46-48, 55 p, 1974.
- [4] M. González, T. Veblen, and J. Sibold, Fire history of *Araucaria –Nothofagus* forests in Villarrica. National Park, Chile, Journal of Biogeography, 32, 1187-1202, 2005.

- [5] M. González, and T. Veblen, Incendios en bosques de *Araucaria araucana* y Consideraciones ecológicas al maderero de aprovechamiento en áreas recientemente quemadas, *Revista Chilena de Historia Natural*, 80(2), 243-253, 2007.
- [6] J. Six, H. Bossuyt, S. Degryze, and K. Denef, A history of research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics, *Soil and Tillage Research*, 79, 7-31, 2004.
- [7] M. Bird, and D.R. Gröcke, Determination of the abundance and carbon isotope composition of elemental carbon in sediments, *Geochimica et Cosmochimica Acta*, 61, 3413– 3423, 1997.
- [8] M. Schmidt, and A.G. Noack, Black carbon in soils and sediments: analysis, distribution, implications, and current challenges, *Global Biogeochemical Cycles*, 14(3), 777–793, 2000.
- [9] P. Högberg, Tansley Review No. 95. ^{15}N natural abundance in soil-plant systems, *New Phytologist*, 17, 9-203, 1997
- [10] L. Saito, D. Miller, R. Johnson, L. Qualls, E. Provencher, and P. Szameitat, Fire effects on stable isotopes in a sierran forested watershed, *Journal Environmental Quality*, 36, 91-100, 2007.
- [11] A. Sala, G. L. Peters, Mc, Intyre, and M. Harrington, Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire, and burning season, *Tree Physiology*, 25, 339-348, 2005.
- [12] C. Rumpel, M. Alexis, A. Chabbi, V. Chaplot, D. Rasse, C. Valentin, and A. Mariotti, Black carbon contribution to soil organic matter composition in tropical sloping land under slash and burn agriculture, *Geoderma*, 130, 34-45, 2006.
- [13] CONAF, Antecedentes sobre impacto de incendios forestales en la IX Región. Documento de visita a la zona afectada por Incendios, Temuco, Chile. 16 pp, 2002.
- [14] J. Amigo, and C. Ramírez, A bioclimatic classification of Chile: woodland communities in the temperate zone, *Plant Ecology*, 136, 9-26, 1998.
- [15] A. Miller, The climate of Chile. In: Schwerdtfeger, W. (Ed.), *Climate of Central and South America*. World Survey of Climatology, Elsevier, Ámsterdam, pp.113-145, 1976.
- [16] Soil Survey Laboratory Staff. Soil survey laboratory manual. Soil Survey Investigations Report No. 42, Version 3.0. USDA-Natural Resources Conservation Service-National Soil Survey Center, Lincoln, NE. 693pp, 1996.
- [17] M.I. Bird, and D.R. Gröcke, Determination of the abundance and carbon isotope composition of elemental carbon in sediments, *Geochimica et Cosmochimica Acta*, 61, 3413– 3423, 1997.
- [18] M. Wilson, *NMR Techniques and applications in geochemistry and soil chemistry*, Pergamon Press, Oxford, pp. 182-216, 1987.
- [19] H. Knicker, P. Müller, and A. Hilscher,, How useful is chemical oxidation with dichromate for the determination of "Black Carbon" in fire-affected soils?, *Geoderma* 142, 178-196, 2007.
- [20] G. Almendros, H. Knicker, and F. González-Vila, Rearrangement of carbon and nitrogen forms in peat after progressive isothermal heating as determined by solid-state ^{13}C - and ^{15}N -NMR spectroscopies, *Organic Geochemistry*, 34, 1559–1568, 2003.

- [21] H. Knicker, G. Almendros, F. J. González-Vila, J. A. González- Pérez, and O. Polvillo, Characteristic alterations of quantity and quality of soil organic matter caused by forest fires in continental Mediterranean ecosystems: a solid-state C-13 NMR study, *European Journal of Soil Science*, 57, 558–569, 2006.
- [22] J. González, F. González, G. Almendros, and H. Knicker, The effect of fire on soil organic matter - a review, *Environment International*, 30, 855– 870, 2004.
- [23] J. Ehleringer, R.N. Buchmann, and L.B. Flanagan,. Carbon isotope ratios in belowground carbon cycle processes, *Ecology Application*, 10, 412–422, 2000.
- [24] S. Macko, M.. Estep, P.. Hare, and T. Hoering, Isotopic fractionation of nitrogen and carbon in the synthesis of amino acids by microorganisms, *Isotope Geoscience*, 65, 79-92, 1987.
- [25] R. Benner, M.L. Fogel, E.K. Sprague, and R.E. Hodson, Depletion of ^{13}C in lignin and its implications for carbon stable isotope nitrogen, *Nature*, 329, 708–710, 1987.
- [26] E. Murage, W. P. Voroney, and R. Beyaert, Turnover of carbon in free light fraction with and without charcoal as determined using the ^{13}C natural method, *Geoderma*, 138, 133-143, 2007.
- [27] H. Knicker, G. Almendros, F. Gonzáles-Vila, F. Martin, and H. Ludermann, ^{13}C - and ^{15}N -NMR spectroscopic examination of the transformation of organic nitrogen in plant biomass during thermal treatment, *Soil Biology & Biochemistry*, 28, 1053-1060, 1996.
- [28] A. Prieto-Fernandez, M. Carballas, and T. Carballas, Inorganic and organic N pools in soils burned or heated: immediate alteration and evolution after forest wildfires, *Geoderma* 121, 291-306, 2004.
- [29] T.H DeLuca, M.G, MacKenzie, M.J. Gundale, and W.E. Holben, *Soil Science Society American Journal*, 70, 448–453, 2006.
- [30] P. Boeckx, L. Paulino, C. Oyarzún, O. Van., Cleemput, and R. Godoy, Soil $\delta^{15}\text{N}$ patterns in old forests of southern Chile as integrator for N-Cycling, *Isotopes in Environmental and Health Studies*, 41(3), 245-259, 2005.
- [31] S. Wan, D. Hui, and Y. Luo, Fire effects on nitrogen pools and dynamics of terrestrial ecosystems: a meta-analysis, *Ecological Applications*, 11,1349–1365, 2001.
- [32] W.W. Covington, and S.S. Sackett, Soil mineral nitrogen changes following prescribed burning in ponderosa pine, *Forest Ecology and Management*, 54, 175–191, 1992.
- [33] O. Zackrisson, M. C. Nilsson, and D.A. Wardle. Key ecological function of charcoal from wildfire in the Boreal forest. *Oikos*, 77, 10-19, 1996.
- [34] N. Fierer, J.P. Schimel, R.G. Cates, and J.P. Zou, Influence of balsam poplar tannin fractions on carbon and nitrogen dynamics in Alaskan taiga floodplain soils, *Soil Biology and Biochemistry*, 33,1827–1839, 2001.
- [35] Glaser B. E. Balashov, L. Haumaier, G. Guggenberger, and W. Zech, Black carbon in density fractions of anthropogenic soils of the Brazilian Amazon region, *Organic Geochemistry*, 31, 669– 678, 2000.

- [36] P. Vitousek, and P. Matson, Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly-pine plantation, *Ecology* 66(4), 1360-1376, 1985.
- [37] M. Yamato, Y. Okimori, I.F. Wibowo, S. Anshiori, and M. Ogawa, Effects of the application of charred bark of *Acacia mangium* on the yield of maize, cowpea and peanut, and soil chemical properties in South Sumatra, Indonesia, *Soil Science Plant Nutrition*, 52, 489–495, 2006.
- [38] M. A Rondon, J. Lehmann, J. Ramírez, and M. Hurtado, Biological nitrogen fixation by common beans (*Phaseolus vulgaris* L.) increases with bio-char additions, *Biology and Fertility of Soil*, 43, 699–708, 2007.
- [39] D. D. Warnock, J. Lehmann, T. Kuyper, M. Rillig, Mycorrhizal responses to biochar in soil – concepts and mechanisms, *Plant and Soil*, 300, 9–20, 2007.

Soil carbon storage in allophanic soils: Study of a temperate pristine rainforest *Nothofagus pumilio* in the altitudinal limit

Francisco Matus^{1,2}, Marcelo Panichini², Roberto Godoy³, Fernando Borie^{1,2}

¹ Departamento de Ciencias Químicas Universidad de La Frontera, Temuco Chile.
E-mail: fmatus@ufro.cl; fborie@ufro.cl

² Programa de Doctorado en Ciencias de los Recursos Naturales, Temuco, Chile.
E-mail: mpanichini@ufro.cl

³ Instituto de Botánica, Universidad Austral de Chile, Valdivia, Chile.
E-mail: rgodoy@uach.cl

Abstract. We present an overview of the factors and mechanisms involved in carbon storage in Chilean allophanic soils with particular reference to porous steeped (30-70% slopes) volcanic materials occurring in the piedmont and dejections cones of the volcano range in Chile. These soils comprehend more than 50% of the volcanic soils area. We discuss the organic carbon stabilization in term of previous research in more well developed soils from agricultural sites in the southern regions of Chile. Rainforest ecosystems in the mountain range (most eastern part) standing on recent substratum, like porous volcanic soil, may become limiting in their carbon and nitrogen retention. Therefore, these ecosystems should present conservation strategies for soil carbon under conditions of high rainfall ($> 5,000 \text{ mm y}^{-1}$) scenarios. In this context Antillanca soil is a black sand scoriaceous basaltic material occurring mainly on the upper slopes of Casablanca and Antillanca volcanoes ($40^{\circ}47'S$, $72^{\circ}12' W$, 920-1,120 m a.s.l.), where the temperate pristine rainforest *Nothofagus pumilio* (Poepp et Endl) stand is close to the treeline. We studied the soil carbon distribution in nine soil profiles as well as some relevant soil properties interacting with carbon preservation through combination of chemical fractionation (Al-organic matter complex, including their recalcitrance) and biological measurements such as microbial biomass and soil carbon mineralization under incubation conditions. We also investigate the protective capacity of these soils, i.e. the upper limit of a soil to store organic carbon. All of these aspects and inferences are presented and discussed from ecological point of view.

1. Introduction

Soil organic matter (SOM) turnover slows down by environmental factors such as low temperature. However, even under these conditions, the mechanisms favouring SOM preservation, including interaction of soil organic carbon (SOC) with clay minerals by physical adsorption via van der Waals forces, electrostatic attraction, cation and anion bridges, sorption of humic substances through polyvalent metal cations of Al^{3+} , Fe^{3+} , and Ca^{2+} , provide the main stabilization processes and may occur very rapidly in milliseconds [1]. These interactions often lead to a positive

and significant relationship between the distinctive clay sized fraction and SOC. However, in Chilean allophanic soils, such relationship has not been found [2,3]. Instead, Al and Fe are strongly correlated with SOC, probably via ligand exchange mechanism. Matus *et al.* [2], pointed out that c.a. 40% of all soil C was like an independent C pool, other than the C associated to the mineral clay (and silt) fraction, indicating that the humic substances associated to Al and Fe complexes should be regarded as an easily measurable SOM pool.

In this paper we present an overview of the mechanisms involved on SOC stabilization in allophanic soils, particularly on those belonging to steeped volcanic soils from the southern temperate rainforest standing on the porous volcanic materials such the Antillanca soil in the National Park of Puyehue. We investigated the stability of the SOC in the top and deep soil layers by combining chemical fractionation [Al-organic matter complex, extracted by Na-pyrophosphate (Al_p , Fe_p) and C measured in the extract, C_p] with the biological activity (microbial biomass and C mineralization). We also assessed the recalcitrance of SOC by the glomalin test. Finally, we studied the protective capacity of these soils (the upper limit of a soil to store SOC) by a theoretical and practical approach.

2. Mechanisms of soil organic C stabilization

Soil C storage is controlled primarily by the input of net primary production (quantity and quality) and by its decomposition rate. Decomposition of organic matter in temperate soils is carried out mainly by soil heterotrophic microbes which constitute about 2-4% of SOC [4]. Abiotic chemical oxidation is likely to account for less than 5% of organic matter decomposition [5]. There is a continuum from undecomposed to very decomposed organic material as a result of biotic oxidation in the early stage of decomposition. In this phase, namely the labile or active phase, the turnover time (the inverse of mean residence time of a molecule in a C reservoir¹) is about 1 to 2 yr and 25-66% of the initial C is lost depending on the chemical nature of organic compounds [4]. The intermediate stage of decomposition accounts for a total loss of about 90% of the initial C (turnover time ca. 10-100 yr) and it is regarded as the transitional organic matter pool [6]. The complete decay process comprises a late stage of decomposition with a turnover time of ca. 100 to more than 1000 yr, accounting for the long-term stabilization of C in soils [6]. The stabilization of soil C can be defined as the processes that contribute to reduce SOC losses and can be achieved by several mechanisms which have recently received a lot of attention due to its importance in the global terrestrial C cycling. Depending

¹ Carbon reservoir: it is the available quantity of soil C for decomposition within one specific compartment (C pool). Any reservoir may evolve through exchanges with the other ones (biogeochemical or geochemical fluxes). Mean residence time is the average time of organic molecule remaining in a biogeochemical reservoir. Assuming that the pool of C at steady state (input SOM = output SOM = dQ/dt) and contains an amount Q of organic matter, the mean residence time $\tau = Q/(dQ/dt)$.

on the nature of soils (volcanic or non-volcanic) one or more of these mechanisms dominate.

The protection of SOC is often used as a generalized term in the specialized literature and involves all mechanisms of SOC stabilization [6]. One of this is the selective preservation of SOC due to recalcitrance, including plant litter, microbial byproducts, rhizodeposition of organic compounds, humic polymers, and charred organic matter. The spatial inaccessibility of organic matter for decomposers due to encapsulation, occlusion, intercalation, hydrophobicity and stabilization by interaction with mineral surfaces (Fe-, Al-, Mn-oxides, phyllosilicates) and metal ions is a form of physical and chemical protection. However, these concepts are far from a complete understanding. For instance, molecular recalcitrance of organic compounds is a relative concept, because it is important during the early stage of decomposition while during the later stage, spatial inaccessibility and organo-mineral interactions acquire more relevance [6]. The main difficulty in predicting SOC dynamics is due to the simultaneous occurrence of the various factors and mechanisms of SOC stabilization [6].

The factors contributing to SOC stabilization are those residing in the soil environment for example, the amount and nature of clay, microbial activity, soil pH, and free Al and Fe. Other external conditions such as temperature and precipitation also play a key role in C stabilization.

2.1. *Stabilization of organic carbon in Chilean allophanic soils*

Chilean volcanic soils are known to contain allophane (about 50% of clay weight) and they are rich in soil organic matter (up to 31%) [3]. Furthermore, they contain also considerable amounts of reactive Al and amorphous Fe and poorly crystallized minerals and oxides, which cause their unique characteristics, e.g. low bulk density and high phosphate retention [2,7]. In general the input of organic matter and decomposition rates are controlled by factors such as climate, drainage and land use, which in turn control the SOM levels. There is also evidence that Al (extracted with Na-pyrophosphate) influences the SOM content in volcanic soils, since a positive and highly significant relationship has been found between these two variables [3,8]. The stabilizing effect of Al is due to complexation with SOC in the soil solution and subsequent precipitation as insoluble Al-SOM complexes, suppressing microbial enzyme activity and substrate degradation [9]. Therefore, there may be a confounding effect between Al, clay content and mineralogy in volcanic soils. The clay fraction in many volcanic soils, rich in Al, Fe and oxides, together with allophanic and imogolite type materials may slow down SOM decomposition [e.g. 9, 10, 11]. Although phyllosilicate clays are considered to play an important role in stabilizing SOM decomposition, studies have pointed out that amorphous Al hydroxides and insoluble organically bond Al rather than allophane (or imogolite type materials) are the key parameters for SOM stabilization [12]. Matus *et al.* [2] showed that extractable Al in acid ammonium acetate, rather than

clay content and climatic factors, controlled the variation of SOC levels in Chilean allophanic soils on a regional scale from southern latitude 36 ° to 42 ° (Table I; Fig. 1). Basile-Doelsh *et al.* [13], however, recently showed that the largest proportion (82.6%) of SOM in the top horizon was associated with minerals in organomineral complexes of imogolite type materials. In contrast, Scheel *et al.* [14] showed that between 13% and 84% of the dissolved organic C (DOC) was precipitated with Al, depending on pH, Al/C ratio and the type of DOC. These results therefore support the idea that both Al and allophanic materials are the major factors for immobilization of SOM in volcanic soils. Aluminium measured in the extract of Na-pyrophosphate at pH 10 is often used to estimate the Al complexed with organic matter. Matus *et al.* [3] examined the effects of Al, silt plus clay content (particles size 0–53 µm) and clay mineralogy on the control of the SOC level in volcanic soils. They found that Al extracted with pyrophosphate (Al_p) was highly correlated with the SOC ($R^2 = 0.62$; $P < 0.01$). They also found that the soluble C measured in the extract of pyrophosphate (C_p) together with clay mineralogy, i.e. the quantity of allophane and its C associated in the silt plus clay fraction, rather than the silt and clay content of soil, controls the largest proportion of variation of SOM across volcanic soils in Chile. Thus, C_p accounted for about 40% of the whole SOC [3]. Therefore, this C pool can be distinguished from the C associated with allophane by a C balance in which the sum of both accounted for most of the whole C in allophanic soils (Matus, unpublished).

Table I Coefficient of determination (R^2) of soil organic C (Mg ha⁻¹) versus mean annual precipitation (MAP), mean annual temperature (MAT), and amounts ha⁻¹ (0–20 cm) of silt, clay, and ammonium-acetate-extractable Al (Al_a) for the investigated soil orders (After [2] with permission from Elsevier)

Soil order	MAP (mm)	MAT (°C)	Silt	Clay (Mg ha ⁻¹)	Al _a	Multiple regression ^a
Alfisol (n = 14)	0.21 ^{ns}	0.21 ^{ns}	0.23 ^{ns}	0.16 ^{ns}	0.65***	0.84**
Andisol (n = 126)	0.09***	0.11***	0.03 ^{ns}	0.02 ^{ns}	0.40***	0.40***
Inceptisol (n = 14)	0.54**	0.53**	0.00 ^{ns}	0.00 ^{ns}	0.88***	0.88***
Ultisol (n = 15)	0.50**	0.54**	0.33*	0.09 ^{ns}	0.55**	0.55**
All (n = 169)	0.21***	0.15***	0.05**	0.14***	0.52***	0.55** ^b

ns= not significant; *, **, *** = significant at $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively

^a Al_a and MAT were the model parameter for Alfisols, and Al_a for other soil orders.

^b $C = 30.79 + 49.70 \times Al_a + 0.021 \times MAP$

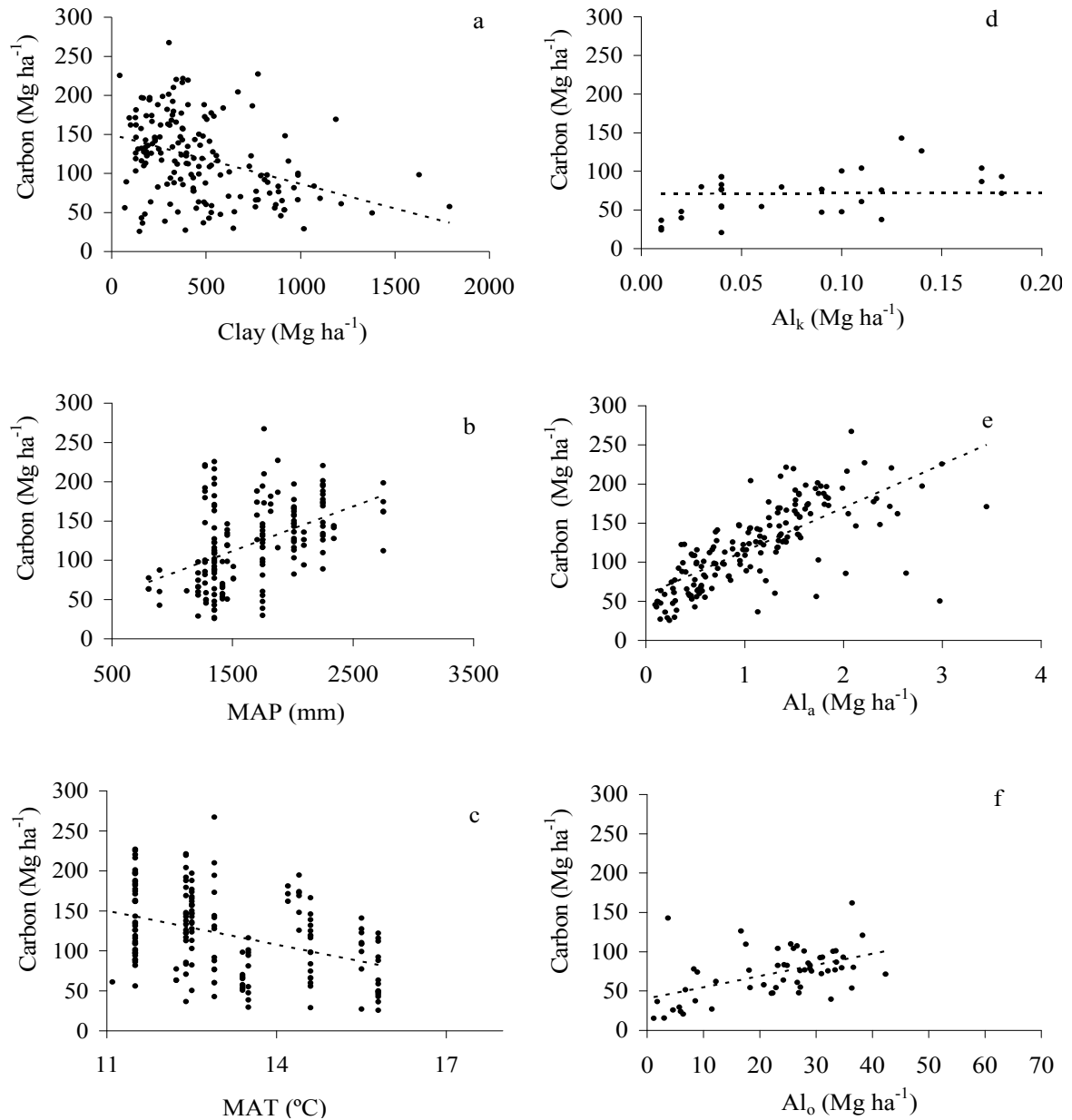


Fig. 1. Relationships from simple regressions between soil organic C and (a) soil clay content, (b) mean annual precipitation (MAP), (c) mean annual air temperature (MAT), (d) KCl-extractable Al (Al_k), (e) acid ammonium acetate-extractable Al (Al_a) and (f) oxalate-extractable Al (Al_o) for samples soils (0-20 cm), $n = 169$ from Table I. Al_k and Al_o were not done for all soil samples (after [2] with permission from Elsevier)

Many researchers have pointed out that ligand exchange (LE) is the major mechanism controlling the sorption of humic substances by variable-charge minerals [1,8,15]. We use Yuan *et al.* [15] model to explain Al-SOM complex formation in our soils. An allophane particle is a hollow spherule with an external diameter of about 3.5-5.0 nm and a wall thickness of approximately 0.7 nm [16]. There are structural defects (0.3 nm wide) within the outer wall where (OH)Al(H₂O) groups occurs (Fig. 2). These groups can attract or loose protons depending on the soil pH because the allophane is regarded as short-range ordered minerals with variable-charge (or pH-dependent). Fig. 2 represents the formation of a surface complex by LE mechanism between a hydroxyl group attached to Al in the allophane spherule and a carboxylate group from HA. The reaction produces a negative charge which is compensated by electrostatic interactions with Na⁺ or Ca²⁺ and perhaps Al³⁺ ions. Thus HA sorption is promoted by the presence of electrolytes such as NaCl and CaCl₂. Soil organic matter bound to spherule of allophane can interact again with Ca²⁺ ions to form a new complex mediated by electrostatic attraction. On an analogous way, an identical mechanism should explain the large quantity of reported C_p [3]. In a recent study, C_p in the silt and clay particles (n = 18 soil samples 0-10 cm) was just about 41% and 88% of the C measured in each fraction, respectively (Matus, unpublished). This finding indicates that C_p is unevenly distributed amongst the fractions and that the physical C in the silt fraction (C associated in the silt minus C_p in the silt) was highly correlated with SOC. From the above-mentioned findings it may be anticipated that LE mechanism is the precursor for further electrostatic interactions to form a new nucleus of Al-SOM complexes that subsequently precipitate. In line with this, Huygens *et al.* [17] studied the link between aggregate and SOC dynamics in a chronosequence (second growth *Nothofagus obliqua* (Mirb.) Oerst forest, grassland and *Pinus radiata* D. Don, plantation) in a Chilean Andisol (0-10 cm). Soil organic C in aggregate was studied using size and density fractionation, $\delta^{13}\text{C}$ analysis and C mineralization experiments. The results showed that electrostatic interaction between amorphous Al and clay minerals was the main mechanism for stabilization of the soil aggregates and this result in the absence of an aggregate hierarchy in this type of soil. Indeed, in our volcanic soils, the allophane content was rather low (< 7% in 0-10 cm, [3]) and LE mechanism should be less important when the correlation between allophane and SOC is weak. Thus, electrostatic sorption and physical protection of SOC and soil aggregates can be the main processes of SOC stabilization and its recalcitrance should not largely affect SOC stabilization [17]. However, when SOM is positive and significantly related with allophane [3] LE should be relevant.

The approach of soil organic matter recalcitrance in Chilean allophanic soils has been studied previously [18]. However, the impact of agricultural practices such as burning crop residues and its effects on the amount of inert C (the so called black carbon, BC) produced by incomplete combustion, has recently been investigated [Matus, unpublished]. The distribution and isolation of the BC in agricultural

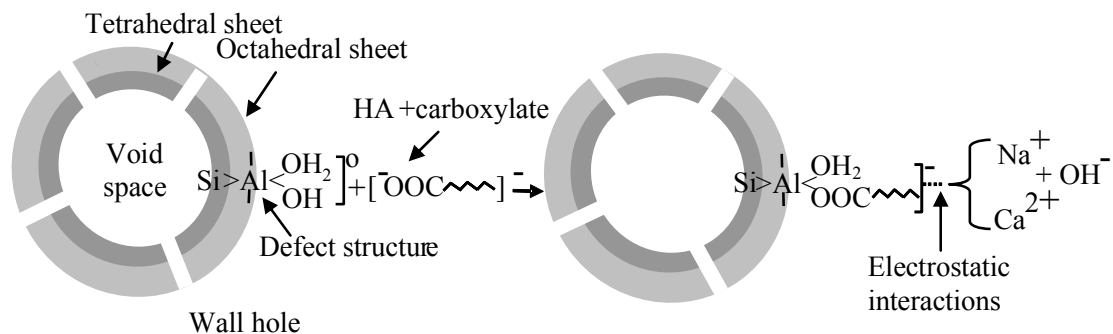


Fig. 2. Ligand exchange mechanism between external allophane spherule of 3.5-5 nm and humic acids (HA) with its carboxylate groups (COOH) which is bound to Na⁺ or Ca²⁺ electrolyte by electrostatic interactions [15] (After B. K. G. Theng, personal communication). Draws are not proportional to the true size structure

allophanic soils was less than 10% of the SOC. Black C composition was studied by ¹³C-NMR spectroscopy. It was seen that there was no differences in aromatics compounds (most functional groups of BC) between burned and unburned treatments 15 years after continuous burning. These results were consistent with those of Rumpel [19] in which no differences were found between a burned and unburned control after 30 years.

On the other hand, Borie *et al.* [20] studied the impact of a glycoprotein termed glomalin. This compound is produced by arbuscular mycorrhizal fungi (AMF) which is recalcitrant to microbial attack and mainly influences soil carbon storage and aggregation. Glomalin originally present in the AMF wall hyphae is secreted into the soil air-water interface and it is currently quantified from soil following an operational definition as glomalin-related soil protein (GRSP) [21]. The basic extraction method involves the use of a citrate buffer at neutral or slight alkaline pH at high temperature [21]. It has been postulated two glomalin fractions: an easily soluble extractable glomalin (EEG) after centrifugation and total glomalin (TG) which is the residue after centrifugation, extracted by citrate solution at pH 8 in the autoclave. The protein content of each fraction is quantified by Bradford assay. In a recent study the glomalin was determined at different soil depths (up to 40 cm) in agricultural soils and in an evergreen forest ecosystem. Surprisingly, the contribution of glomalin to the total amount of soil carbon in forest soils ranged between 19% and 26% and in the agricultural soils between 7% and 9%. Glomalin decreased as soil depth increased [22]. Nowadays, glomalin extraction has been criticized, because the method is unspecific to quantify this glycoprotein [23].

In conclusion, the most important mechanisms in Chilean allophanic soils appears to be a ligand exchange to form the primary complexes [24] which in turn promote electrostatic attractions of cations such as Ca²⁺, Na⁺ and Al³⁺ to form stable soil aggregates. Ligand exchange should be less important when allophane is weakly or not related to the SOC as it is the case in our study of Antillanca soils (see below).

2.2. *Protective capacity of soil organic matter in allophanic soils*

Hassink [25] observed that the quantity of soil C in the silt and clay fraction (0-20 μm) of long-term Dutch temperate arable and grassland sandy soils (differing markedly in its SOM content) was similar, suggesting that soils have an upper limit of C saturation, determined by their capacity to protect organic matter by adsorption processes. When the protective capacity is fulfilled, further C addition is not longer stabilized by the silt and clay fraction and thus C accumulates in the sand-size fractions (20-2000 μm), enhancing C and N mineralization [26,27]. However, soils under different land-use managements may reach the effective carbon stabilization (ECS) which is a saturation level smaller than the protective capacity due to factor other than physico-chemical adsorption. The ECS may be regarded as the threshold value for soils to act either as carbon sink or source, comparing soils within the same land-use managements [Matus unpublished]. The protective capacity of a soil can be assessed by plotting the total soil C versus the C in the physical fractions [Matus unpublished]. For the clay-sized particles in temperate soils an asymptotic response can be expected, indicating that further increases in the soil C are no longer reflected by an increase of SOM in this fraction. However, in volcanic soils the quantity of silt or clay (or both) is not related to SOC, but complexed with Al and Fe. Therefore, we pose the question if the volcanic soils can reach the protective capacity and how this limit can be envisaged.

From [3,28] it can be calculated that one mol of Al_p can complex 8.3 moles C_p , i.e. 0.12 (= 1/8.3) moles of Al can complex one mole of C_p . Dahlgren and Ugolini [29] established a strong linear relationship between pyrophosphate-extractable C and organically complexed Al and Fe ($\text{Al}+\text{Fe}$)_p ($R^2 = 0.97$; $P < 0.001$). Assuming that most Al_p and Fe_p was extracted from humus complexes, these data indicated that Al and Fe form metal-humus complexes with a metal:carbon atomic ratio of 0.18 (the slope of the regression). According to Higashi *et al.* [30], a theoretical calculation from previous literature can be made and a ratio of 0.12 should be regarded as the saturation of humic substances with metals. When this ratio is exceeded, the metals will not be longer complexed by humic substances and it will then be available for synthesis of inorganic components like allophane and imogolite type materials [29]. Therefore, we addressed these and other related matters in a study case of Antillanca's soils in the next section.

3. Study case of Antillanca

3.1. *Introduction*

More than 2.5 million ha (50% of the total volcanic soils in Chile) occur on steep slopes within the limits of the Andean ranges between latitude 36° and 47°. The landforms associated with these soils range from moderately steeped to precipitous; however, slopes between 30-70% predominate. The prevalence of steep landforms is due to the late tertiary history of uplift and tilting of land surfaces, associated with

the Andean orogeny [31]. On this land basement, volcanoes through their successive eruptions had deposited several deep mantles of volcanic ash which in part have been reduced by anthropogenic and natural erosion. Many of the Chilean volcanoes in this area are currently active, associated with the regional climate and plant covering. Stepped soils, most are derived from basaltic materials date from recent eruptions which formed dejection cones from sloppy piedmonts in the volcanoes leaving a large area of scoriaceous porous soils. Vegetation in these ecosystems is evergreen formation composed with species such as: *Laureliopsis philippiana* Loseer, *Aextoxicum punctatum* R. et Pay, *Drimys winteri* J. R. et G. Forster and *Nothofagus* sp [32]. In the upper altitudinal limit *Nothofagus pumilio* (Poepp et Endl Krasser) can be found close to the treeline (1,000-1,120 m a.s.l.). An example of this ecosystem is Antillanca's soils in the Puyehue National Park resulting from activities of the Casablanca and Antillanca volcanoes. The mean annual precipitations in this ecosystem is $> 5,000 \text{ mm yr}^{-1}$ with snow covering during June to November, with the mean annual temperature of 4.5°C ranging between -8.7°C to 24.8°C inside the forest. In this area three experimental sites were established, differentiated by tree density and height [33,34], where the distribution of SOM in the uppermost and subsoil has not been studied.

The aims of this study were to examine: i) the distribution of soil C in the Antillanca soil and the stability of SOC in its profile; ii) the biological activity and its relationship with the stabilizing agent such as Al- and Fe-SOM complex and iii) the protective capacity of the soil, i.e. the upper limit of a soil to store SOM.

3.2. Methodology

3.2.1. Experimental site description

The present study was carried out in an experimental microcatchment dominated by *Nothofagus pumilio* forest types in southern Chile ($40^{\circ}47'S$, $72^{\circ}12' W$, 1,120 m a.s.l.) with a mean annual precipitation ($>5,000 \text{ mm}$) whose chemistry still reflects the pre-industrial conditions [32]. Thus, the productivity of the ecosystem depends on the internal cycling of soil organic C. Three sites were selected where *N. pumilio* forest has a mean height of 9, 13 and 23 m, and a stand density of 5,900, 3,600 and 1,734 trees ha^{-1} effectively, namely Site 1, Site 2 and Site 3, respectively. The average tree age was about 120 yr. The understory is dominated by *Drimys andina* (Reiche). Rodr. et Quez. and *Maytenus disticha* (Hook. F.) Urban [32]. *N. pumilio* is an important and representative deciduous tree in Chile and has a wide latitudinal distribution over approximately 2,000 km, reaching from latitude 35° to 55° [35]. This species grows mainly at high altitude, close to the treeline at both sides of the mountain range 'cordillera de los Andes' and 'cordillera de la Costa'. Soil samples were taken by core cylinder from horizons A, AC and C at Site 1, Site 2 and Site 3 from three soil pedons excavated up to 100 cm depth, spaced each other for about 10 m. A total of 27 soil samples for analysis and 27 soils cores for bulk density

were collected by pushing a steel cylinders with a known volume (5 x 8.2 cm) into the undisturbed soil. Soil characteristics are presented in Table II.

3.2.2. Chemical analysis

All soils were analysed for pH in water using a 1:2.5 soil:solution ratio. For the Al, Fe and Si extraction, air dried samples were used in duplicate. For a detailed description of this extraction method see [3]. The following analyses were conducted: (a) oxalate extraction (Al_o , Si_o and Fe_o), (b) pyrophosphate extraction (Al_p and Fe_p), (c) allophane content and (d) particle size analysis as described by [36]. Carbon determination in the whole soil and in the pyrophosphate extract (C_p) was determined in two replicates using potassium dichromate [Matus *et al.*, in press].

3.2.3. Carbon stabilization and protective capacity

Soil C stability was examined by plotting the carbon stability ratio, C_p :SOC versus SOC. The two variables, C_p and SOC are strongly correlated (see Fig. 6c) and therefore we minimize the risk of plotting spurious correlation which take place when the denominator of a ratio (in this case SOC) is used in both axis x and y in a regression line. On the other hand, the protective capacity of soils has been defined as the upper limit of soil C associated with the physical fraction of silt and clay particles in non-volcanic temperate soils [25]. We use this approach by plotting C_p , expressed as $g\ kg^{-1}$ soil against the corresponding whole SOC content on a normalized scale. This enabled us to compare all soil pedons developed under similar climate conditions. An asymptotic relationship is expected where no longer SOC can be complexed (stabilized) by Al and Fe to form C_p . The level of soil C at which this saturation takes place was called critical SOC level, determined by a graphical statistical tool (see data analysis).

The recalcitrance of SOC was assessed by glomalin (a glycoprotein resistant to microbial decomposition). This was evaluated in Site 1 and Site 3 in one pedon only. The extraction involved the use of citrate buffer at neutral or slight alkaline pH at high temperature in the autoclave. The EEG, easily extractable glomalin is obtained by autoclaving 1 g of soil mixed with 20 mM citrate at pH 7.0 for 30-60 min. The solution containing the glomalin is separated by centrifugation (10,000 x g for 10 min). The residue is exhaustively extracted with 50 mM citrate solution at pH 8.0 for 60-90 min at 121°C in the autoclave and this was TG (total glomalin). In each fraction the protein content is quantified in a spectrophotometer using the Bradford assay (Bio-Rad Protein Assay Catalog 500-0006) [22].

Table II Soil characteristics (average of three pedons per site \pm standard error of the mean) in *Nothofagus pumilio* forest of southern Chile

Site	Soil horizons cm	Bulk density Mg m ⁻³	SOC ¹ stock Mg m ⁻²	Soil pH _{water}	Sand ²	Silt ²	Clay ²	Allophane ³
----- (g kg ⁻¹ soil) -----								
1	A (0-11)	0.71 ± 0.04	6.1 ± 3.8	5.9 ± 0.10	760	160	80	23 ± 0.6
	AC (11-51)	0.90 ± 0.04	15.0 ± 7.8	6.2 ± 0.10	860	80	60	37 ± 6.4
	C (51-100)	0.92 ± 0.03	12.3 ± 3.2	6.2 ± 0.10	820	120	60	30 ± 1.6
	Total stock		34.3 ± 4.9					
2	A (0-16)	0.56 ± 0.04	9.4 ± 1.9	6.1 ± 0.30	740	180	80	21 ± 1.8
	AC (16-36)	0.79 ± 0.09	9.4 ± 2.6	6.0 ± 0.03	700	220	80	42 ± 2.3
	C (36-100)	0.99 ± 0.03	10.7 ± 3.0	6.1 ± 0.10	840	80	80	27 ± 5.8
	Total stock		29.5 ± 2.5					
3	A (0-19)	0.54 ± 0.06	11.0 ± 2.44	5.6 ± 0.10	740	180	80	21 ± 1.5
	AC (19-41)	0.74 ± 0.04	8.1 ± 8.1	5.9 ± 0.01	760	180	60	43 ± 6.1
	C (41-100)	0.92 ± 0.05	19.6 ± 8.2	6.1 ± 0.03	860	80	60	41 ± 9.3
	Total stock		38.7 ± 6.2					

¹Soil organic carbon

²One replicate only

³Calculated as [3]

3.2.4. *Microbial biomass and carbon respiration*

Microbial biomass C and C mineralization rates were estimated in all pedons from Site 1 and Site 3. Microbial biomass was estimated by the fumigation-extraction method using a $K_e = 0.38$ [37] in all soil depth and results were expressed on an oven-dry soil basis. For fumigation, liquid ethanol free CHCl_3 was used. Soil organic carbon in $\text{K}_2\text{S}_2\text{O}_8$ extracts from fumigated and unfumigated samples was

analyzed using a dichromate oxidation [Matus *et al.*, in press]. Carbon mineralization rates were carried out by mixing 50 g of soil (dry weight basis), sieved through 0.005 m mesh size and moistened to a water potential of -33 kPa. The soil was placed in a 2 liters airtight glass jar containing a vial with 10 mL of 0.5 M NaOH and incubated at 22 °C (± 2 °C) in the dark during 1, 3, 7 and 15 days. At each sampling time, trapped CO₂ was precipitated as carbonate with excess 0.75 M BaCl₂ and excess NaOH was back titrated automatically with 0.5 M HCl to reach pH 8.3 [38]. At each sampling time, a new vial containing NaOH was placed into the glass jar. The rate of carbon mineralization was calculated as:

$$\frac{dy}{dt} = k(h - y) \quad (1)$$

where: $\frac{dy}{dt}$ is the C mineralization rate (mg CO₂ 100 g⁻¹ soil d⁻¹) and y is an asymptotic exponential model:

$$y = h(1 - e^{-kt}) \quad (2)$$

Where y is the cumulative soil respiration, h the maximum C respired, k the constant rate (day⁻¹) and t the incubation time (days). To obtain the C mineralization rates we first estimate the h and k by non-linear regression by successive iteration using the chi-square for each parameter (h and k) as a function of the iteration number. These values give information to optimize the parameters (optimization means reducing the chi-square value as much as possible). The fitting for each incubated soil was done using CurveExpert release 1.37.

3.2.5. Data analysis

Comparison of multiple means for SOC distribution, microbial biomass and soil C respiration rates for all horizons at each site to test differences amongst the means (average of three pedons) was carried out by the least significant difference (LSD) using Tukey-Kramer HSD (honestly significant difference test). All statistical analyses were computed using the JMP statistical software (SAS Institute, Cary, NC, U.S.A.). The critical SOC level to look at the C saturation of the soils was essayed by the 'Cate-Nelson split' technique [39] by plotting the C_p in ordinate and SOC in abscissa. Differences in C_p values (if any) were found by clustering the data points in two groups with maximum statistical homogeneity within the groups to maximize the chi-square test. Graphically C_p values are separated by placing a vertical line intersecting a horizontal line that maximize the numbers of data points in the first (left bottom) and third (right top) quadrants I and III, respectively (see Fig. 6c). The vertical line intersecting the abscissa is regarded as the critical SOC level in which additional organic matter cannot form more C_p. The critical SOM best separates the high from low C_p groups. Statistically the vertical line represents the highest R² that accounts for the observations into two population groups at the postulated critical level of SOC.

3.3. Results and general discussion

First, we present a general morphological description of the studied soils based on Mella and Kühne [40] and Wright et al. [31], together with our own observations. Secondly, we discuss the SOC distribution and its stabilization, including the C saturation concept. Thirdly, we linked all above-mentioned findings with measured biological activities.

3.3.1. General soil description

At all sites a partially decomposed litter layer (4-5 cm) was observed. The top mineral A horizon (for the thickness of each horizon of the three sites see Fig. 4) is dark brown (10YR 3/3, moist) with loamy sand texture, non-sticky and non-plastic, friable with granular structure and abundant fine roots. The middle horizons (AC) is gray (10 YR 5/1, moist), loamy sand with fine scoriaceous gravel, friable with non recognizable structure, non-sticky and non-plastic. Finally, the C horizon is very dark gray (2.5 YR 3/0, moist) loamy sand to coarse sand, partially cemented, with an appreciable amount of pomes (Fig. 3a). At all sites and profiles we found visually identifiable zones in the form of light brown 'hot spots' in the AC horizons (Fig.3b). These zones have been described as small, spatially separated soil areas in the profile with distinct physicochemical properties; young SOM depleted in ^{15}N and high microbial biomass [41, 42]. Our hot spots seem to be hydrophobic, because they were drier than the soil samples from the adjacent soil matrix, having abundant albic fungal hyphae. This spots are being studied for chemical characteristics as well.

3.3.2. Soil organic matter, microbial biomass and carbon mineralization

Soil organic carbon is the result of long-term accumulation of recalcitrant humified C, interacting with the soil mineral phase, microbial community and soil depth. Our questions were addressed to gain information about SOM storage in these porous materials and what are the mechanisms and factors operating on its accumulation.

On average, for all horizons, the SOC ranged from 30 to about 120 g kg⁻¹ soil and there were significant differences amongst sites. Soil organic matter contents amongst pedons were highly variable and, therefore scarce differences in depth horizons were observed, although more distinctive quantity of C was measured in the top soil (Fig. 4). These differences were expected because a large root volume was observed in the top soil. Fontaine *et al.* [43] recently focused a study on the recalcitrance of SOM. In the surface layer (A horizon) the supply of fresh C by plants (litters and exudates) enables microbial biomass to decompose the recalcitrant C compounds, otherwise stored over long-time period (>1000 yr). When fresh-C is available at deep soils by illuviation, leaching, incorporation by earthworms and termites (pedoturbation), recalcitrant humus can be available for soil microbes promoting extra C mineralization called priming effect [43]).

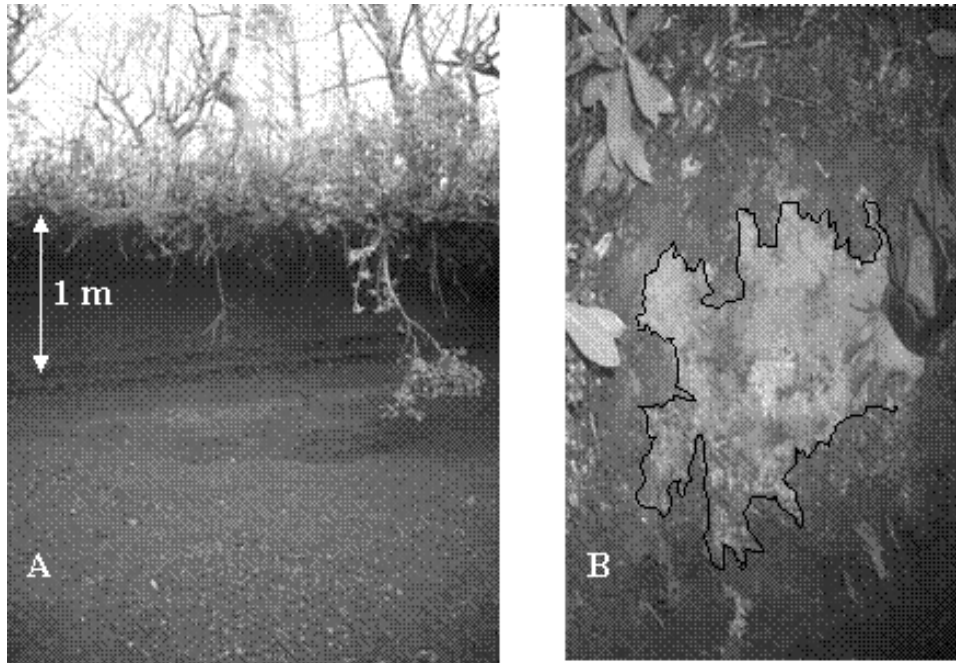


Fig. 3. Site 1 of Antillanca showing (A) the soil profile and (B) the ‘hot spots’ in the AC horizon in *Nothofagus pumilio* forest of Southern Chile

In the present study, microbial biomass as the percentage of SOC ranged between 2.5% and 4% of the whole SOC, the normal range found in the literature [4] (Fig. 5a and 5b). Soil C mineralization rates were also calculated and they decreased as the time of incubation increased (Fig. 5c and 5d). However, both, microbial biomass and mineralization rates were not significantly different in the top and deep soils. Assuming that the microbial community and the efficiency of soil C use by microbial biomass does not change (because the clay content was similar across soil site and depth (Table I), [44]), our results suggest that the active (or labile) organic matter pool, either for the surface and deep soil were comparable. With high stability of SOM in deep soils less labile C and less microbial biomass should be expected. It is also possible that the priming effect may compensate the stability of SOC in deep soils, because vertical transfer of fresh C can be important.

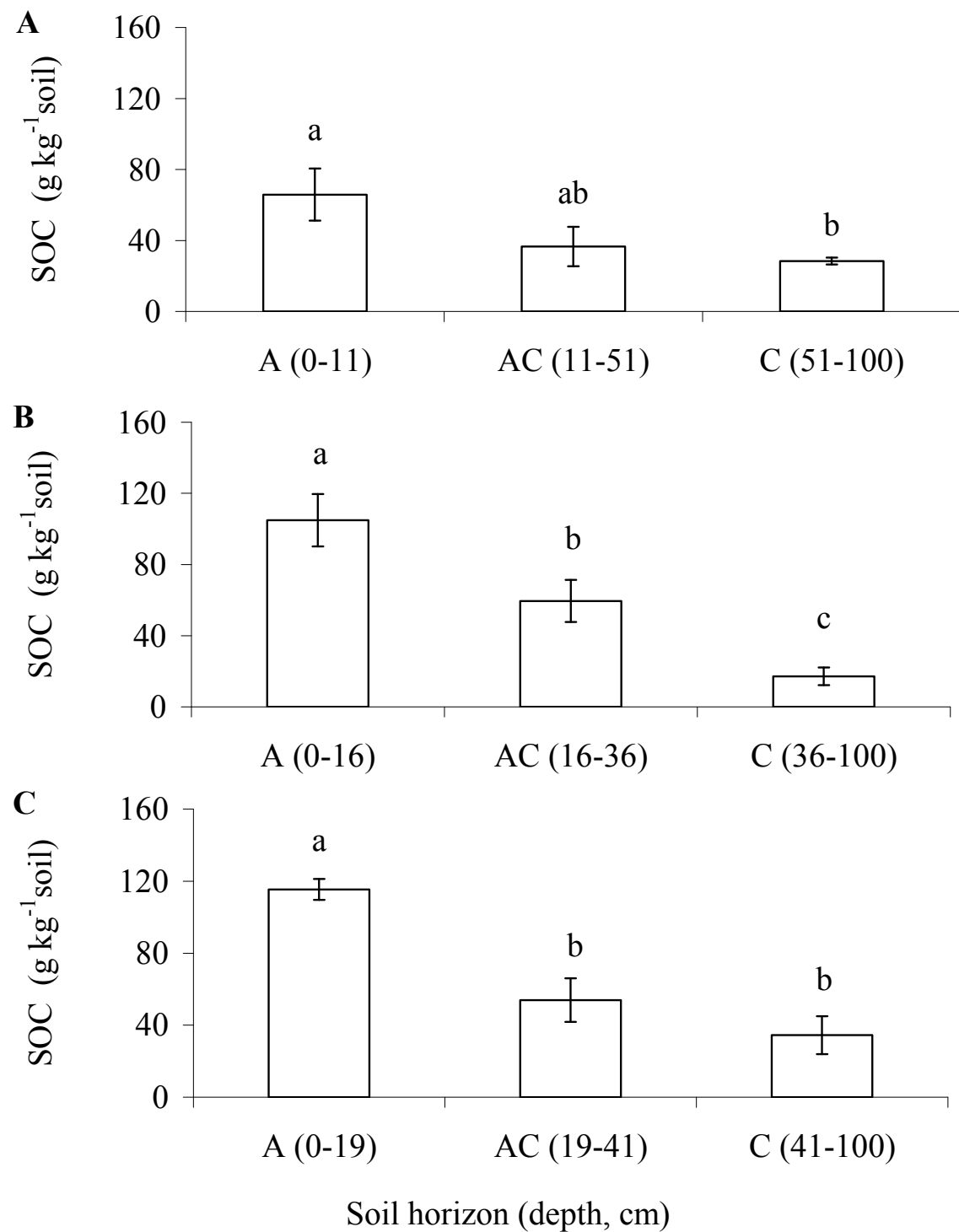


Fig. 4. Soil organic C (SOC) distribution (average of three pedons) along the profile of Antillanca soil for (A) Site 1, (B) Site 2 and (C) Site 3. of *Nothofagus pumilio* forest of Southern Chile. Bars followed by the same letter indicates not significant differences at *P* level 0.05. Vertical line on top of each bars indicate the standard error of the mean

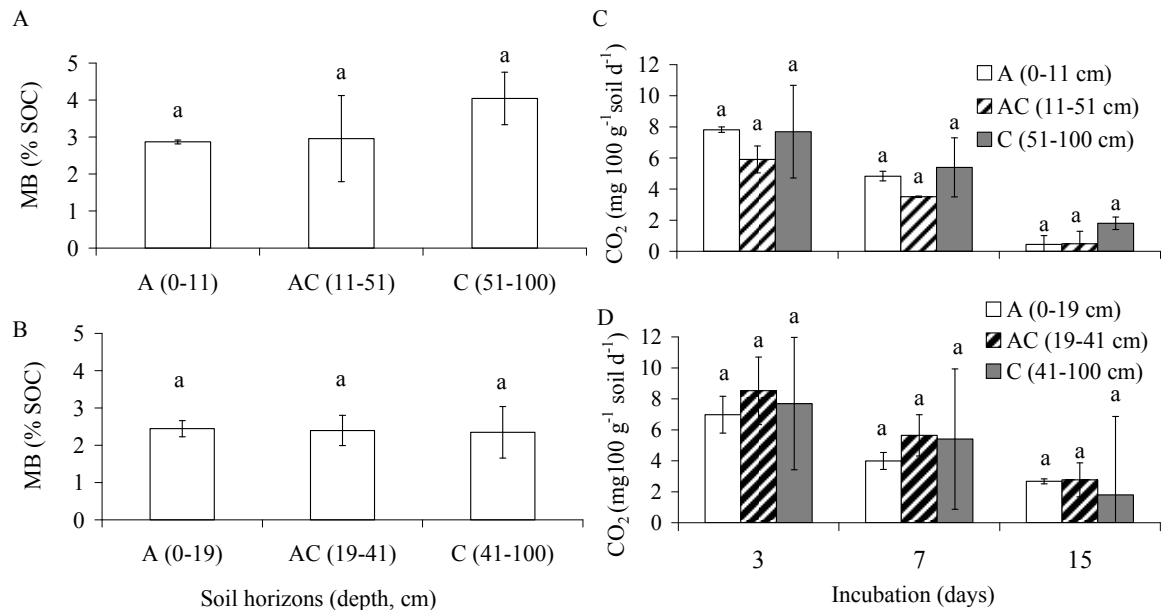


Fig. 5. Microbial biomass (MB) fumigation-extraction (average of three pedons) as percentage of soil organic carbon (SOC) for (A) Site 1 and (B) Site 3. Soil carbon mineralization rate for (C) Site 1 and (D) Site 3 of *Nothofagus pumilio* forest of southern Chile. Bars followed by the same letter for MB and for C mineralization at the same time of incubation, indicate not significant differences at P level 0.05

3.3.3. *Stability ratio and protective capacity*

There was a weak correlation between the weight of the physical silt- and clay-fractions and SOC content of the soils. Similar results were observed between allophane and SOC. Therefore, the stability of organic matter was assessed by extraction of Al and Fe with Na pyrophosphate, which reflects the metals complexed with SOM and by determining the glomalin content, as indicator of SOM recalcitrance [22]. The pyrophosphate extraction of Al_p and Fe_p and its relationship with SOC and C_p is shown in Fig. 6. Firstly, Al_p ($y = -7.2 + 250.3x - 113.4x^2$, $R^2 = 0.88$, $P < 0.01$) and Fe_p ($y = -35.1 + 494.6x - 399x^2$, $R^2 = 0.88$, $P < 0.01$) were well related with SOC, indicating that Al and Fe complex with humic substances explained most of the variation of the SOC level. Note that the best fit for both Al_p and Fe_p was a quadratic regression, suggesting that no more SOC can be complexed with metals beyond 0.5% and 0.35% (eye guessing) Al and Fe, respectively (Fig. 6a and 6d). The metal in excess is the Al and Fe extracted from other sources (such as minerals structure free of SOM, gibbsite and interlayered Al) [30,45]. Similar results were obtained between Al_p ($y = 3.4 + 54.7x - 15.9x^2$, $R^2 = 0.86$, $P < 0.01$) and Fe_p ($y = -4.54 + 121.5x - 91x^2$, $R^2 = 0.89$, $P < 0.01$) versus C_p (Fig. 6b and 6e). The critical level of SOC is shown in Fig. 6c, at which no more Al- and Fe-SOM complex can be formed. According to the graphical split technique the C_p values are best separated at 80 g kg^{-1} of SOC. On the other hand, Dahlgren and Ugolini [29] related C_p values with $(Al+Fe)_p$ and they found a positive and significant relationship with a slope of 0.18 representing the atomic ratio $(Al+Fe)_p/C_p$. According to Higashi et

al. [30] theoretically, it seems impossible that organic matter can bind metallic ions at ratios higher than 0.12. In our case the regression between C_p and $(Al+Fe)_p$ for all soil samples was $y = 0.12x - 0.0027$, $R^2 = 0.85$, $P < 0.01$. However, the slopes for the individual horizons A, AC and C were: 0.13, 0.071 and 0.078 (Fig.6f). This indicates that humus in the top soils is fully saturated with metals, but subsoils are still far (40%) from this limit. This means that pyrophosphate extract a C_p partially saturated and any metals produced by weathering will be either complexed with SOM or it will go to form allophane [30]. Our results were also supported by the literature [29,30]. Differences such as origin and type of SOM and pH may be combined to vary the complexing ability of humic substances between different soils and vegetation types, making the ratio somehow, variable. However, for any given soil and horizon, a ratio may exist which corresponds to the saturation of the humic complex with metals [29].

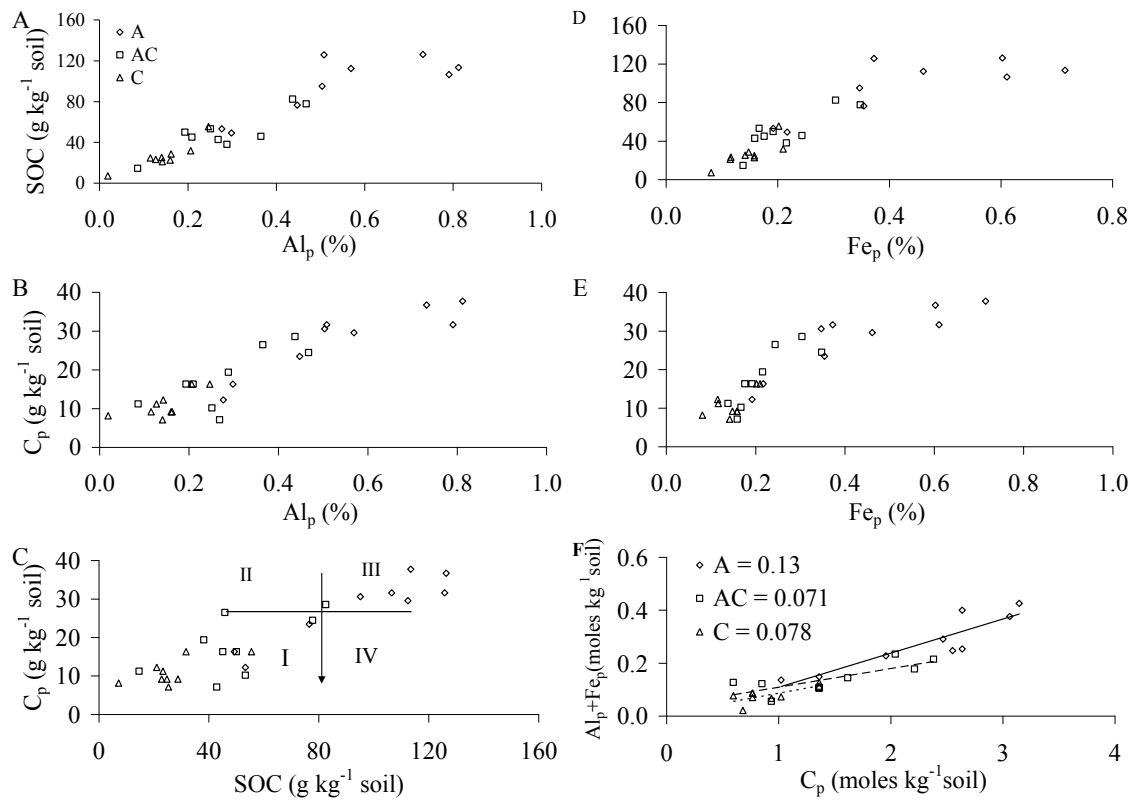


Fig. 6. Relationship between (A) Al_p and (D) Fe_p (both metals extracted in pyrophosphate) and soil organic C (SOC) and (B) Al_p and (E) Fe_p with the carbon extracted by pyrophosphate (C_p). Relationship between (C) SOC and C_p. The arrow on abscissa indicates the critical level of SOM at which no more C_p is formed. Relationship between atomic ratios (F) C_p and $(Al+Fe)_p$ for all soil samples of Antillanca from *Nothofagus pumilio* forest of southern Chile. The slope of the regression is shown for each horizons

Secondly, we related the amount of SOC with the stability ratio (C_p :SOC) (Fig. 7), provided that both variable are correlated (Fig. 6c). The ratio ranged between 0.17 and 1, showing more stability of SOC in deep horizons. Although, the fitted quadratic model ($y = 0.65 - 0.0087 + 5E-05x^2$, $R^2 = 0.37$, $P < 0.01$) was significant (data point = 1 was not considered) there was a weak relationship, because the differences disappear when the ANOVA test was run per horizons (data not shown). This was consistent with lack of significance for microbial biomass and C mineralization rates. Indeed, there was no relationship at all between the stability ratio and the C mineralization rates of the soils.

On the other hand, total glomalin content for Site 1 ranged between 11 and 12 g kg⁻¹ soil and for Site 3 between 7 and 13 g kg⁻¹ soil. Easily extractable glomalin for Site 1 varied between 2 and 5 g kg⁻¹ soil and for Site 3 between 2 and 7 g kg⁻¹ soil. Contrary to what we found for TG in deep soils, EEG decreased across the soil profile. Here, TG was lower when compared with other studies. Total glomalin was

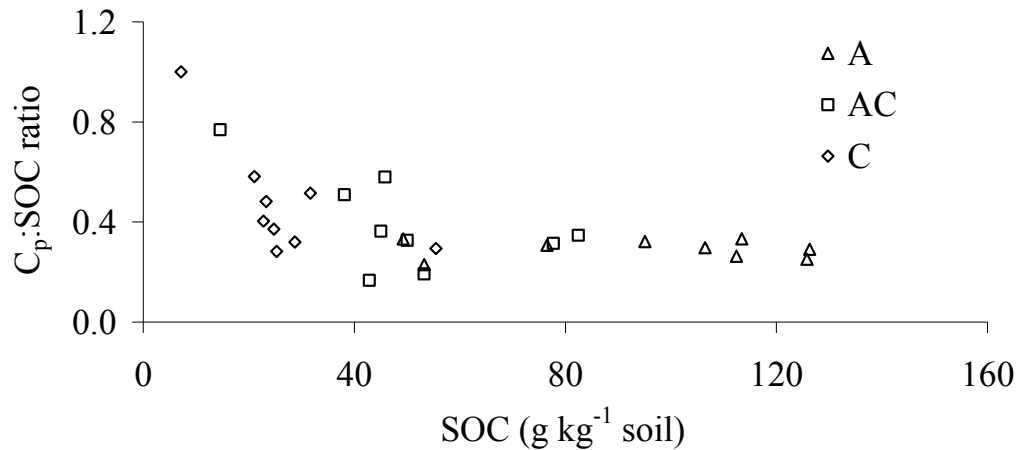


Fig. 7. Relationship between SOC and the stability ratio C_p :SOC for all samples of Antillanca's soils from *Nothofagus pumilio* forest of Southern Chile

21 times lower than that reported for evergreen forests in a well developed volcanic soil of Chile [22]. In our study, although, statistical analysis could not be performed, the results indicate that TG as percentage of whole SOC tended to be high in deep soil. However, EEG did not show a consistent pattern (data not shown).

3.4. Summary and conclusions

We conducted a study in an Antillanca soil, being a scoriaceous and porous allophanic soil, weakly developed from dejection cones of Antillanca and Casa Blanca volcanoes. In this area *Nothofagus pumilio* is the dominant forest species. We studied the soil organic C stability by combining chemical (Al, Fe and C extracted in pyrophosphate and recalcitrance of soil carbon by glomalin test) and biological methods (microbial biomass and C mineralization rates) in nine soil samples

profiles distributed in three sites of different tree density and height (the same altitudinal level 1,120 m a.s.l.). We found that Al and Fe extracted by pyrophosphate explained much of the SOC variation. However, SOC stabilization, assessed by the stability ratio of the C extracted in pyrophosphate and the C in the whole soil was similar, either for the top and deep horizons. The recalcitrance of SOM measured by glomalin, did not show reliable results. These findings were consistent with the fact that, despite of the soils horizons: i) microbial biomass as percentage of the whole soil C and ii) C mineralization rates were similar. Furthermore, there was no relationship between C mineralization rates and the stability ratio, indicating that the stabilization of soil organic C was at the same extent in all soils and depth. It seems that humus bound to metals (Al and Fe) represented by the C extracted in pyrophosphate is limited at a critical level of SOC of 80 g kg⁻¹ soil, beyond which no more complex can be formed. This was consistent with the fact that the atomic ratio of (Al+Fe):C (all extracted in pyrophosphate) was close to 0.12 (the theoretical limit for C saturation with metals [30]). However the humus in the subsoil seems to be less saturated with Al and Fe.

4. Final remarks

The soil organic carbon reservoir corresponds to 615 Gt C in the top 0.2 m and 2,344 Gt C at depths of up to 3 m [46]. This is particularly important in Chilean allophanic soils, where organic matter can be reached up to 31%. The mean residence time of soil organic carbon strongly increases with soil depth, reaching a range of 2,000–10,000 yr in deep soils [43]. However, little is known about the factors and mechanisms controlling the stability of carbon in deep soils [42,43]. The response to climate change, especially in pristine unpolluted forest, remains uncertain. For instance, about 50% of the allophanic soils area in Chile is found on steep slopes in the limits of the Andean ranges between latitude 36° and 47° (mostly covered by evergreen forest formation). At southern latitude the mean precipitation may reach more than 5,000 mm per year in sandy soils (this study) where percolation, bioturbation and leaching push down soil organic matter to deep soil horizons. It seems that SOM recalcitrance is of minor importance and ligand exchange and electrostatic interaction acquire relevance as the main mechanism of soil carbon stabilization. In this area, there are also other well developed soils [3] but, water retention capacity can be easily exceeded and anoxic conditions can be generated. Besides soil organic C dynamics, this may influence other nutrients such as nitrogen. Under anoxic soils conditions, retention by dissimilatory nitrate reduction to ammonium plays a key role in the preservation of bioavailable nitrogen in this forest [47]. On the other hand, Al and Fe not only have a functioning in the chemistry of soil C complexation and allophane formation, but also may play a role in nitrate reduction to ammonium under anoxic conditions [48]. In fact, Fe in the green rust (a mixture of reduced Fe²⁺ and Fe³⁺) has been reported to reduce nitrate to ammonium at neutral pH under anoxic conditions as well [49].

The results of our study in Antillanca soils have several implications. First, they suggest that the mechanisms that protect soil organic carbon below the top soil of fresh carbon appear to be the same and provide an interesting strategy of this ecosystem to maintain nutrient recycling when they move to a deep soil. Second, our incubation results suggest that, even under favorable conditions of moisture and temperature for microbial biomass, soil organic carbon from the deep soil layer provides sufficient energy to sustain microbial populations active. Third, the existence of global increase of temperature may accelerate the decomposition of this large pool of deep carbon, in contradiction to the predicted effect based on ancient buried carbon being more stable with low mineralization rates. Finally, the existence of a finite capacity to store SOM (protective capacity) is relevant, because the soils can act as source or sink, depending on the degree of carbon saturation. It appears imperious to study whether the C associated to the physical fraction of clay are saturated with SOM or not. The top soils in this study apparently are more saturated than the subsoils and this may favor the vertical transport of organic material to the subsoils showing similar stabilization than top soils. Therefore, improved knowledge of these factors and mechanisms is essential to determine whether the nutrient will react to global change impact and how we are globally going to face this problem in these type of soils

Acknowledgements

The authors would like to thank Nicolás Pacheco from the Forestry National Corporation (CONAF) for his competent support in the field and Noelia Sepúlveda for her skilful assistance in laboratory. We also acknowledge to FONDECYT project N° 1080065 from the National Commission for Science and Technology (CONICYT) for its financial support. Our recognition to Professor Oswald Van Cleemput from Gent University for his valuable comments on early version of this paper.

References

- [1] D. L. Spark, "Environmental soil chemistry", Academic Press 352 pp, 2003.
- [2] F. Matus, X. Amigo and S. M. Kristiansen, "Aluminium stabilization controls organic carbon levels in Chilean volcanic soils", *Geoderma*, 132, 158–168, 2006.
- [3] F. Matus, E. Garrido, N. Sepúlveda, I. Cárcamo, M. Panichini and E. Zagal, "Relationship between extractable Al and organic C in volcanic soils of Chile", *Geoderma*, 148, 180-188, 2008.
- [4] D. S. Jenkinson and J. N. Ladd, "Microbial biomass in soil: measurement and turnover". In: *Soil Biochemistry* (E. A. Paul and J. N. Ladd, Eds.), pp. 415–471. Marcel Dekker, New York, 1981.
- [5] P. Lavelle, E. Blanchart, A. Martin, S. Martin, A. Spain, F. Toutain, I. Barois and R. Schaefer, "A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics", *Biotropica*, 25, 130–150. 1993.

- [6] M. von Lützow, I. Kögel-Knabner, K. Ekschmitt, E. Matzner, G. Guggenberger, B. Marschner and H. Flessa, “Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions - a review”, *European Journal of Soil Science*, 57, 426–445, 2006.
- [7] S. Shoji, R. Dahlgren and M. Nanzyo, “Classification of volcanic ash soils” *In: Volcanic ash soils, Genesis, Properties and Utilization* (S. Shoji, M. Nanzyio and R. A. Dahlgren Eds.), *Development in Soil Science* N° 21, Elsevier, Amsterdam, pp 73-100, 1993.
- [8] H. J. Percival, R. L. Parfitt and N.A. Scott, “Factors controlling soil carbon levels in New Zealand grassland: is clay content important?”, *Soil Science Society of America Journal*, 64, 1623–1630, 2000.
- [9] P. Sollins, P. Homann, and B. A. Caldwell, “Stabilisation and destabilisation of soil organic matter: mechanisms and controls”, *Geoderma*, 74, 65–105, 1996.
- [10] H. Zunino, F. Borie, S. Aguilera, J. P. Martin and K. Haider, “Decomposition of ¹⁴C-labelled glucose, plant and microbial products and phenols in volcanic ash-derived soils of Chile”, *Soil Biology Biochemistry*, 14, 37–43, 1982.
- [11] R. L. Parfitt, A. Parshotam and G. J. Salt, “Carbon turnover in two soils with contrasting mineralogy under long-term maize and pasture, *Australian Journal of Soil Research*, 40, 127–136, 2002.
- [12] J-P. Boudot, “Relative efficiency of complexed aluminium, noncrystalline Al hydroxide, allophane and imogolite in retarding the biodegradation of citric acid, *Geoderma*, 52, 29–39, 1992.
- [13] I. Basile-Doelsch, R. Amundson, W. E. E. Stone, D. Borschneck, J. Y. Bottero, S. Moustier, F. Masin and F. Colin, “Mineral control of carbon pools in a volcanic soil horizon”, *Geoderma*, 137, 477–489, 2007.
- [14] T. Scheel, C. Dörfler and K. Kalbitz, “Precipitation of dissolved organic matter by aluminium stabilizes carbon in acidic forest soils”, *Soil Science Society of America Journal*, 71, 64–74, 2007.
- [15] G. Yuan, B. K. G. Theng, R. L. Parfitt and H. J. Percival, “Interactions of allophane with humic acid and cations”, *European Journal of Soil Science*, 51, 35-41, 2000.
- [16] P. L. Hall, G. J. Churchman and B. K. G. Theng, “Size distribution of allophane unit particle in aqueous suspensions”, *Clays and Clay Minerals*, 33, 345-349, 1985.
- [17] D. Huygens, P. Boeckx, O. Van Cleemput, C. Oyarzún and R. Godoy “Aggregate and soil organic carbon dynamics in South Chilean Andisols”, *Biogeosciences*, 2, 159–174, 2005.
- [18] S. M. Aguilera, I. U. Pino, C de la P. Reyes and M. M. Caiozzi, “Efecto de la materia orgánica en la disponibilidad de fósforo, hierro, cobre y cinc en un suelo de Osorno”, *Agricultura Técnica*, 52, 422-425, 1992.
- [19] C. Rumpel, “Does burning of harvesting residues increase soil carbon storage?”, *Journal of Soil Science and Plant Nutrition*, 8, 44-51, 2008.
- [20] F. Borie, R. Rubio, J. L. Rouanet, A. Morales, G. Borie and C. Rojas, “Effects of tillage systems on soil charactectics, glomalin and mycorrhizal propagules in a Chilean Ultisol”, *Soil Tillage Research*, 88, 253-261, 2006.

- [21] M. C. Rillig, "Arbuscular mycorrhizae, glomalin and soil aggregation", *Canadian Journal of Soil Science*, 84, 355-363, 2004.
- [22] A. Morales, C. Castillo, R. Rubio, R. Godoy, J. L. Rouanet and F. Borie, "Niveles de glomalina en suelos de dos ecosistemas del sur de Chile", *Journal of Soil Science and Plant Nutrition*, 5(1) 37-45, 2005.
- [23] M. C. Rillig, S. F. Wright, K. A. Nichols, W. F. Schmith and M. S. Torn, "Large contributions of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils", *Plant and Soil*, 233, 167-177, 2001.
- [24] H. Appelt, N. T. Coleman and P. F. Pratt "Interactions between organic compounds, minerals, and ions in volcanic-ash-derived soils: I. Adsorption of benzoate, p-OH benzoate, salicylate, and phthalate ions", *Soil Science Society of America Journal*, 39, 623-627, 1975.
- [25] J. Hassink, "The capacity of soils to preserve organic C and N by their association with clay and silt particles", *Plant and Soil*, 191, 77-87, 1997.
- [26] F. Matus, C. Lusk, and C. Maire, "Effects of soil texture, carbon input rates, and litter quality on free organic matter and nitrogen mineralization in Chilean rain forest and agricultural soils", *Communication in Soil Science and Plant Analysis*, 39, 187-201, 2008.
- [27] C. E. Stewart, A. F. Plante, K. Paustian, R. T. Conant and J. Six, "Soil Carbon Saturation: Linking concept and measurable carbon pools", *Soil Science Society of America Journal*, 72, 379-392, 2008.
- [28] R. Dahlgren, S. Shoji and M. Nanzio, "Mineralogical characteristics of volcanic soils" *In: Volcanic ash soils, Genesis, properties and Utilization* (S. Shoji, M. Nanzio and R. A. Dahlgren Eds.), *Development in Soil Science* N° 21, Elsevier, Amsterdam, pp 101-143, 1993.
- [29] R. A. Dahlgren and F. C. Ugolini, "Distribution and characterization of short-range-order minerals in Spodosols from the Washington Cascades", *Geoderma*, 48, 391-413, 1991.
- [30] T. Higashi, F. de Coninck and F. Gelaude, "Characterization of some spodic horizons of the campine (Belgium) with dithionite-citrate, pyrophosphate and sodium hydroxide-tetraborate", *Geoderma*, 25, 131-142, 1981.
- [31] C. A. Wright, "Report to the government of Chile on the volcanic ash soils of Chile", *Food and Agriculture Organization of the United Nations*, Rome, p. 201, 1965.
- [32] R. Godoy, C. Oyarzún and J. Bahamondes, "Flujos hidroquímicos en un bosque de *Nothofagus pumilio* en el Parque Nacional Puyehue, sur de Chile", *Revista Chilena de Historia Natural*, 72, 579-594, 1999.
- [33] R. Godoy, C. Oyarzún and V. Gerding, "Precipitation chemistry in deciduous and evergreen *Nothofagus* forest of southern Chile under a low-deposition climate", *Basic and Applied Ecology*, 2, 65-72, 2001.
- [34] C. Oyarzún, R. Godoy, A. De Schreijver, J. Staelens and N. Lust, "Water chemistry and nutrient budget in an undisturbed evergreen rainforest of southern Chile", *Biogeochemistry*, 71, 107-123, 2004.
- [35] R. Hildebrandt-Vogel, R. Godoy and A. Vogel "Subantarctic-Andean *Nothofagus pumilio* forest", *Vegetatio*, 89, 55-68, 1990.

- [36] F. J. Matus, A. Osorio, A. Acevedo, S. Ortega and R. Cazanga, “Efecto del manejo y algunas propiedades del suelo sobre la densidad aparente”, *Journal of Soil Science and Plant Nutrition*, 2, 7-15, 2002.
- [37] E. D. Vance, P. C. Brookes, D. S. Jenkinson, “An extraction method for measuring soil microbial biomass C”. *Soil Biology and Biochemistry*, 19, 703-707. 1997.
- [38] R. C. Dalal, “Simple procedure for the determination of total carbon and its radioactivity in soils and plant materials”, *Analyst*, 101, 151-154, 1979.
- [39] R. B. Jr. Cate, and L.A. Nelson. “A simple statistical procedure for partitioning soil test correlation data into two classes”, *Soil Science Society of America Proceedings*, 35, 658-659, 1971.
- [40] A. Mella and A. Kühne, “Sistemática y descripción de las familias, asociaciones y series de suelos derivados de materiales piroclásticos de la zona central-sur de Chile”, *In: Tosso, J. (Ed.), Suelos Volcánicos de Chile. Instituto de Investigaciones Agropecuarias, Chile*, pp. 549–716, 1985.
- [41] M. Bundta, F. Widmer, M. Pesaro, J. Zeyer and P. Blasera “Preferential flow paths: biological ‘hot spots’ in soils”, *Soil Biology and Biochemistry*, 33, 729-738, 2001.
- [42] A. Chabbi, I. Kögel-knaber and C. Rumpel “Stabilized carbon in subsoil horizons is located in spatially distinct parts of the soil profile”, *Soil Biology and Biochemistry*, 41, 256-261, 2009
- [43] S. Fontaine, S. Barot, P. Barré, N. Bdioui, B. Mary and C. Rumpel, “Stability of organic carbon in deep soil layers controlled by fresh carbon supply”, *Nature*, 8, 277-280, 2007.
- [44] J. Hassink and A. P. Whitmore, “A model of the physical protection of organic matter in soils”, *Soil Science Society of America Journal*, 61, 131, 1997.
- [45] K. Kaiser and W. Zech, “Defects in estimation of aluminum in humus complexes of podzolic soils by pyrophosphate extraction”, *Soil Science*, 161, 452–458, 1996.
- [46] E. G. Jobbágy and R. B. Jackson, “The vertical distribution of soil organic carbon and its relation to climate and vegetation”, *Ecological Applications*, 10, 423–436, 2000.
- [47] D. Huygens, P. Boeckx, P. Templer, L. Paulino, O. Van Cleemput, C. Oyarzún, C. Müller and R. Godoy, “Mechanisms for retention of bioavailable nitrogen in volcanic rainforest soils”, *Nature Geoscience*, 1, 543-548, 2008.
- [48] H. Y. Huang, T. C. Zhang, P. J. Shea and S. D. Comfort, “Effects of oxide coating and selected cations on nitrate reduction by iron metal”, *Journal of Environmental Quality*, 32, 1306–1315, 2003.
- [49] F. Trolard and G. Bourrie, “Geochemistry of Green Rusts and Fougerite: a reevaluation of Fe cycle in soils, *Advances in Agronomy*, 99, 227-288, 2008.

The old-growth forests in the Valdivian Andes: Composition, Structure and Growth

Pablo J. Donoso¹, Leah Samberg², María Paz Hernández¹, Bastienne Schlegel¹

¹Department of Silviculture, Universidad Austral de Chile, Casilla 567, Valdivia, Chile,
Email: pdonoso@uach.cl

²Department of Environmental Studies, University of California, Santa Cruz, CA 95064,
USA

Abstract. In this contribution the aim was to analyze the information on composition, structure and growth obtained from 180 plots and several transects sampled in two contrasting Valdivian old-growth rainforests, with the objective of having a comprehensive understanding of their ecology and dynamics as a necessary basis for conservation or management. Apparently the difference in aspect of these two forests has been the main driver of their differences in composition, structure and growth: a) the south-aspect forest (TEMATR) has abundant *M. planipes* trees, almost absent in the north-aspect forest (COMATE), and lacks *N. dombeyi* which is important throughout in the COMATE forest in its biomass contribution and in providing a strong vertical stratification, b) canopy trees in the TEMATR double the radial growth of trees in the COMATE forest, c) regeneration in the TEMATR forest is 5 times more abundant than in the COMATE forest, and d) canopy gaps are more frequent and larger in the COMATE forest. These dramatic differences between both old-growth forests suggest that aspect may have a stronger influence on forest dynamics than it has been thought before.

1. Introduction

The dynamics of old-growth forests in the Valdivian Andes has been intensively studied since the first works leaded by Veblen [1,2,3]. His work was focused in *Nothofagus*-dominated forests that included *N. dombeyi* and *N. nervosa* at mid elevations and *N. pumilio* at higher elevations. Otherwise, little has been done in these forests in terms of describing their composition, structure and growth, except for the work by Donoso et al. [4] on the first two issues. Here we report the variable composition, structure and growth of two old-growth forests at the same elevation in San Pablo de Tregua, an experimental property of the Universidad Austral of Chile in the Valdivian Andes, and discuss their variations and how they can affect productivity and potential forest management. This paper is a synthesis of the work that the main author has conducted in San Pablo de Tregua during the last four years and that has already been partially published [5,6,7]. The objective was to have a comprehensive understanding of the ecology and dynamics of these forests as a necessary basis for their conservation or management.

2. Methods

2.1 Study area

The study area is located in the Chilean Andes between 750 and 800 m of elevation in the San Pablo de Tregua experimental forest (39° 38' S, 72° 05' W) of the Universidad Austral de Chile. In this region the typical old-growth forests are those of the Coigüe-Rauli-Tepa forest type [8,9], which is widespread between 500 and 1,000 m asl in the Andes of South-Central Chile, where either Coigüe or Raulí, or both, occupy emergent tiers, and the conifer *Saxegothaea conspicua* (Lindl.), plus the hardwoods *L. philippiana* and *Dassyphyllum diacanthoides* (Less.) occupy the main canopy tier [10,1,2,3,4,11].

In this region both large-scale and small-scale disturbances are common, and are largely described in several sources [e.g. 12,1,2,3,13,11]. Here we studied two old-growth forests of the Coigüe-Rauli-Tepa forest type [8,9] without evidence of past human disturbances. One stand is dominated by the emergent *N. dombeyi*, and *L. philippiana* and *S. conspicua* are the two main canopy species (*Nothofagus*-dominated forest, named COMATE). This stand was established after patchy blowdown by a windstorm [5], as previously reported by [3] for forests of this type elsewhere in the region. This is the most common species composition in old-growth forest stands of this forest type in the Andes of Chile [10,4,1,2,3,11] although *N. nervosa* may also be present. The other stand is dominated by three canopy species, *L. philippiana*, *S. conspicua* and *D. diacanthoides*. It lacks the emergent *Nothofagus* and has a high density of *Myrceugenia planipes* trees in the understory (mixed-species forest, named TEMATR). The *Nothofagus*-dominated stand is in the transition phase of biomass accumulation described by [14], while the mixed-species stand is in the steady-state phase of biomass accumulation [6]. This stand without *Nothofagus* is rare in the region.

Soils are deep and well-drained and are derived from Pleistocene and recent volcanic ash layers in a mountainous area of the Andes range [15,3]. A west-coast maritime climate with a mild temperature range dominates the area, and high annual precipitations (mainly rainfall) that exceed 5,000 mm are common [10,3].

2.2 Sampling

2.2.1. Composition and structure

In both stands we set up 0.05 ha circular plots, regularly spaced every 40 m along linear and parallel transects separated by 40 m from one another, unless the point hit a gap, in which case the plot was located in the next 40 m. We set up 80 plots in part of a 62-ha COMATE forest stand, and 100 plots in the 18-ha TEMATR forest stand. The COMATE stand is located in a terrain with a mean slope of 11% and a predominant north aspect; the TEMATR stand has a predominant south aspect with

a mean slope of 16%. In each plot, we measured all living trees ≥ 5 cm diameter at breast height (dbh, 1.3 m) or above buttresses in the case of *N. dombeyi*. We estimated tree density and basal area for each plot and stand. From that data we were able to describe the tree composition and diameter structure of each stand.

2.2.2. Growth

For growth analysis, the center tree of the species *L. phillipiana* or *S. conspicua* was cored in each plot (one core per tree for diameters < 20 cm, and two perpendicular cores per tree for larger trees). Each measured tree was classified as in the canopy (which included upper main canopy and lower main canopy trees, i.e. trees that had at least half of the crown height exposed to direct sunlight) or in the understory (which included below main canopy and overtopped, i.e. trees with less than half of the crown exposed; *sensu* [1]. Radial growth was compared between forests, species and canopy position through ANOVA. Growth for all combinations of species and canopy position was also compared through ANOVA and a Least Significant Difference (LSD) *a posteriori* test.

2.2.3. Living and dead tree biomass

In each plot we estimated living biomass and Coarse Woody Debris (CWD) in order to compare this variable between both forests and with other temperate forests. This is the first report on CWD in the Andes of Chile, and is reported in [6].

2.2.4. Regeneration

Tree regeneration was evaluated according to two substrates: soils and logs. In each forest four 500 m long transects were followed. Where a fallen log > 20 cm in diameter and 100 cm long was intercepted, regeneration was measured in 1 m² of the surface of this log (with 1 to 4 plots when necessary), and in four 0.25 plots on the soils in the neighborhood of the log (but without its influence). A total of 138 and 104 sampling units were measured in the COMATE and TEMATR forests. Abundance by species was recorded for seedlings (5 - < 50 cm) and saplings (50-200 cm). The importance value (sum of relative frequency and relative abundance divided by 2) of tree species according to height category and substrate was also estimated. Statistical analyses were conducted with the Kruskal-Wallis *H* and Mann-Whitney *U* tests. This information on regeneration is reported in detail in [7].

2.2.5. Canopy gaps

The intercepted length of canopy gaps along the transects described above was recorded in each forest, and 23 gaps chosen randomly in each forest were described in accordance to traditional approaches for extended gaps.

3. Results

3.1. Composition and Structure

Both forests were similar in their abundance and sizes of *L. Philippiana* and *S. conspicua* trees. However, the TEMATR forest with south aspect had a large proportion of small trees of *M. Planipes* (the main *Mirtaceae* species in this area), had a higher density and basal area in *D. diacanthoides*, and nearly lacked *N. dombeyi*. The COMATE forest, on the other hand, in north aspect had a great amount of basal area with few scattered trees of *N. dombeyi*, nearly lacked *M. planipes* and had a lower density and basal area of *D. diacanthoides* (Fig. 1). Both forests statistically differed in number of trees (more in TEMATR), basal area (less in TEMATR) and QMD (greater in COMATE (Table I). This can be largely explained by the great abundance of *M. Planipes* trees in the TEMATR forest and the additive basal area effect that occurs in these forests when *N. dombeyi* trees occupy an emergent position above the canopy tier [see 5]. The two forests have diameter distributions that resemble a reverse J (Fig. 1), although the normal distribution of *N. dombeyi* in the COMATE forest with a mean around 150 cm creates a shape in the distribution closer to a rotated S when all species are graphed together. This does not occur with the group of shade-intolerant species in the TEMATR forest since this is largely composed of *N. nervosa* trees under 55 cm in dbh, and few *N. dombeyi* and *Weinmannia trichosperma* trees of >100 cm.

Table I. Number of trees and basal area ha⁻¹ by species and total per type of old-growth forest in San Pablo de Tregua in the Valdivian Andes

Species	COMATE		TEMATR	
	Trees	Basal Area (m ²)	Trees	Basal Area (m ²)
<i>N. dombeyi</i>	14	40,9	1	3,1
<i>L. philippiana</i>	282	29,1	202	38,5
<i>S. conspicua</i>	154	53,4	100	49,9
<i>D. diacanthoides</i>	43	3,4	65	21,3
<i>M. planipes</i>	1	0,01	225	2,9
Other	9	0,12	13	0,72
Total	501	126,9	606	116,4

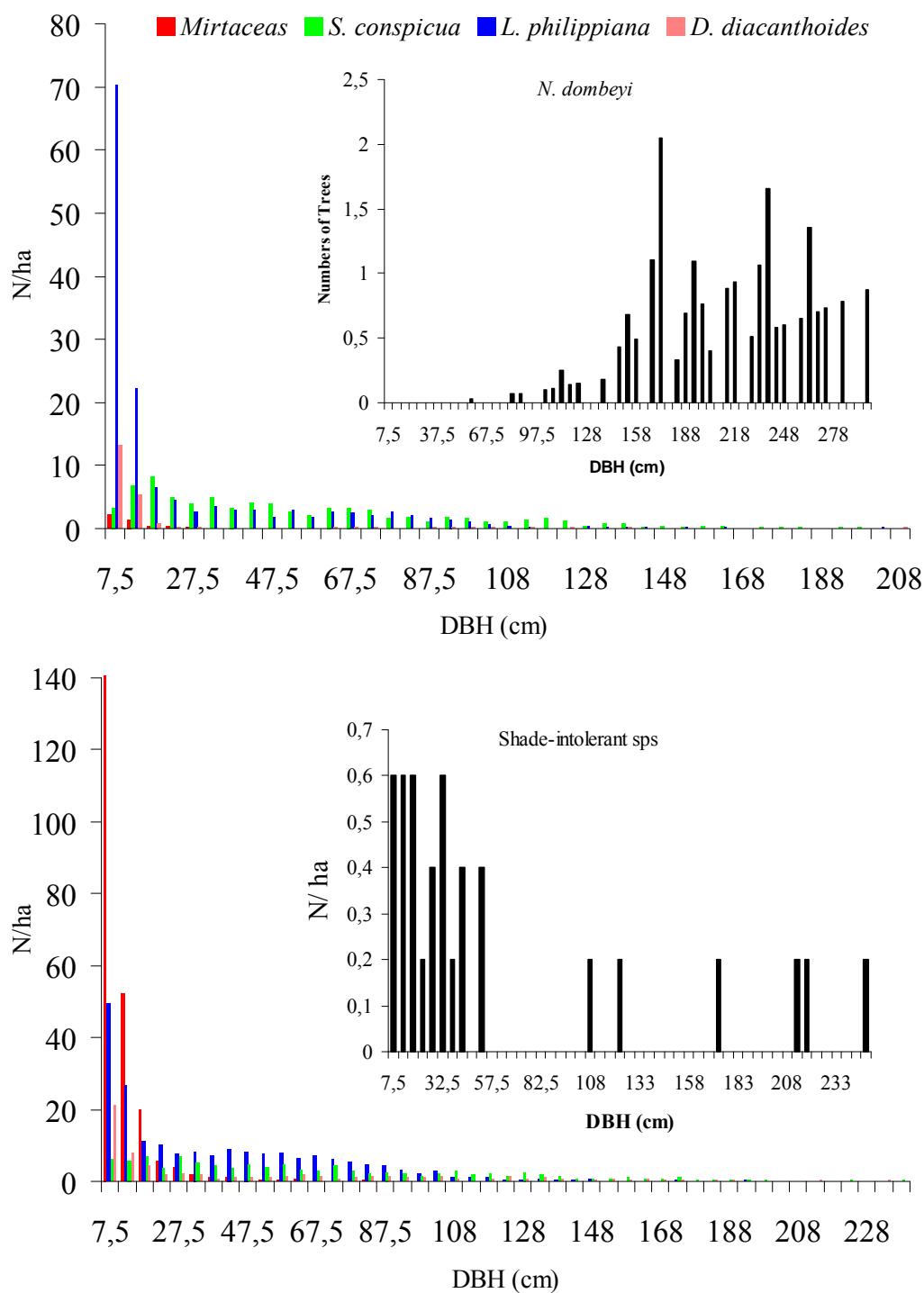


Fig. 1. Diameter distributions by species in the TEMATR (upper figure) and the COMATE forest (lower figure) in San Pablo de Tregua, Valdivian Andes. Canopy species are shown in the main graph and shade-intolerant species in the inset graph. In the COMATE forest the only shade-intolerant species was *N. dombeyi*; in the TEMATR forest also there were a few small trees of *N. nervosa*, one *W. trichosperma* tree, and few *N. dombeyi* trees.

3.2. Growth

Radial growth significantly differed between both forests ($p < 0.0001$), but did not differ between species ($p = 0.5014$). Trees in upper canopy position marginally differed in growth from those in lower canopy position ($p = 0.0562$). No interaction of these factors was significant. The radial growth for each species by canopy position and forest is shown in Table II, which shows that growth for almost all combinations was greater in the TEMATR forest (except between lower canopy *S. conspicua* in TEMATR and upper canopy *L. philippiana* in COMATE).

Table II. Growth results according to forest, species, and canopy position in the two sampled old-growth forests in the Valdivian Andes

Forest	Canopy Position	Mean dbh (cm)	Species	N	Growth (mm)	St. Dev. (mm)	LSD test
TEMATR	Upper	54.06	<i>L. philippiana</i>	46	1.7818	0.7336	A
TEMATR	Upper	59.79	<i>S. conspicua</i>	21	1.8081	0.8040	A
TEMATR	Lower	17.97	<i>L. philippiana</i>	26	1.5605	0.7654	A
TEMATR	Lower	33.45	<i>S. conspicua</i>	4	1.6542	1.1665	AB
COMATE	Upper	55.06	<i>L. philippiana</i>	19	1.0552	0.5441	BC
COMATE	Upper	51.01	<i>S. conspicua</i>	23	1.0208	0.6521	C
COMATE	Lower	15.54	<i>L. philippiana</i>	19	0.9003	0.2316	C
COMATE	Lower	23.60	<i>S. conspicua</i>	23	0.6008	0.3109	C

3.3. Regeneration

The TEMATR forest had much more regeneration than the COMATE forest (67,400 seedlings and 8,800 saplings vs. 12,400 seedlings and 2,400 saplings respectively; Table III). The composition of tree species regeneration in these forests is similar to that observed for large trees (Fig. 2). In the TEMATR forest the highest important values for regeneration were shared between *L. philippiana* and *M. planipes*. In the COMATE forest, on the other hand, regeneration was mainly of *L. philippiana*. In both forests regeneration of *N. dombeyi* was scarce, but it was relatively more important and occurred in more diverse conditions in the COMATE forest. In the COMATE forest there was a significantly larger number of *S. conspicua* seedlings on the soil compared to those on logs; among saplings *L. philippiana* had significantly more growing on the soil substrate, whereas *D. diacanthoides* had more on logs. In the TEMATR forest there were no significant preferences for any substrate among seedlings or saplings of any species (Table III).

Table III. Mean density in 1 m² plots and standard error for regeneration of tree species in each forest on different substrates (soil and log), and statistical results for the Kruskal-Wallis *H* test (* *p* < 0,05, ** *p* < 0,01, *** *p* < 0,001, NS = no significant effect, df = 1 and df = 2) and Mann-Whitney U a posteriori test.

Species	Substrate		Kruskal-Wallis test	
	Soil	log	H	p
COTEMA				
Seedlings				
<i>D. diacanthoides</i>	0,05 ± 0,05	0,04 ± 0,02	2,64	NS
<i>L. philippiana</i>	3,31 ± 0,46	3,02 ± 0,43	0,05	NS
<i>M. planipes</i>	0,01 ± 0,01	0,01 ± 0,01	0	NS
<i>N. dombeyi</i>	0,01 ± 0,01	0,03 ± 0,02	1	NS
<i>S. conspicua</i>	0,02 ± 0,01	0,20 ± 0,06	7,64	**
Total density	3,4 ± 0,47	3,34 ± 0,44	0,12	NS
Saplings				
<i>D. diacanthoides</i>	0 ± 0	0,03 ± 0,01	4,01	*
<i>L. philippiana</i>	0,55 ± 0,10	0,26 ± 0,07	8,82	***
<i>M. planipes</i>	0,01 ± 0,01	0 ± 0	1,01	NS
<i>N. dombeyi</i>	0 ± 0	0,02 ± 0,02	0,99	NS
<i>S. conspicua</i>	0 ± 0	0,01 ± 0,01	0,99	NS
Total density	0,56 ± 0,10	0,32 ± 0,07	5,22	*
TEMATR				
Seedlings				
<i>D. diacanthoides</i>	0,05 ± 0,02	0,11 ± 0,04	1,25	NS
<i>L. philippiana</i>	0,26 ± 0,08	0,24 ± 0,08	0,17	NS
<i>M. planipes</i>	0,24 ± 0,07	0,17 ± 0,06	0,66	NS
<i>N. dombeyi</i>	0 ± 0	0,01 ± 0,01	1,00	NS
<i>S. conspicua</i>	0,13 ± 0,08	0,04 ± 0,02	0,00	NS
Total density	0,67 ± 0,14	0,57 ± 0,12	0,08	NS
Saplings				
<i>D. diacanthoides</i>	0 ± 0	0 ± 0	0	NS
<i>L. philippiana</i>	0,06 ± 0,04	0,01 ± 0,01	1,03	NS
<i>M. planipes</i>	0,05 ± 0,04	0,08 ± 0,04	1,30	NS
<i>N. dombeyi</i>	0 ± 0	0 ± 0	0	NS
<i>S. conspicua</i>	0 ± 0	0 ± 0	0	NS
Total density	0,11 ± 0,05	0,13 ± 0,04	1,13	NS

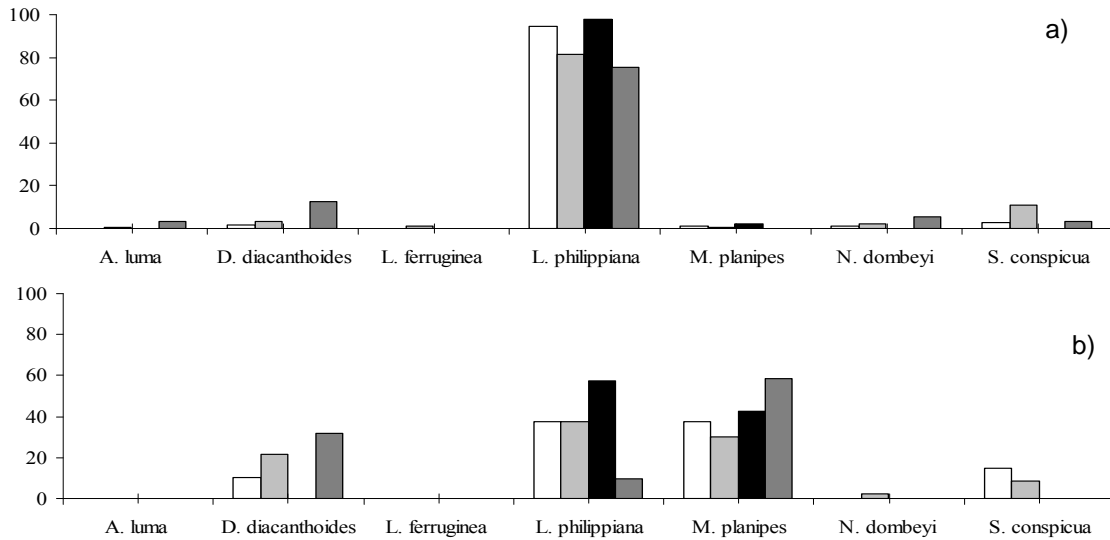


Fig. 2. Importance values for tree species regeneration according to height class (seedlings and saplings), and type of substrate (soil and log) in the COMATE (a) and TEMATR (b) forests; for each species the order of bars is seedlings on soil (white), saplings on soil (light gray), seedlings on logs (black) and saplings on logs (dark gray)

3.4. Living and dead tree biomass

Detailed data on biomass of living trees and CWD is reported in [6], but here we provide general information to integrate this variable within the context of the other characteristics of these forests and reported above. Living tree biomass and CWD were greater in the COTEMA forest. Living tree biomass was greater because both basal area was greater (Table I) and trees were on average taller due to the presence of the *N. dombeyi* trees that were about 45 m in height. The basal area of *N. dombeyi* in the COMATE forest was additive to (and not at the expense of) that of the canopy trees [5]. Dead tree biomass or CWD was also greater in the COMATE forest, and this was explained mostly by the greater biomass of snags in this forest (Table IV). The species composition of CWD was also different between both forests: *N. dombeyi* represented two thirds of the CWD in the COMATE forest, with only 11% in *L. Philippiana* and *S. conspicua*, while these two species represented one half of the CWD in the TEMATR forest.

Table IV. Estimated above-ground biomass (EAGB), log and snag biomass, and overall Coarse Woody Debris (CWD, logs and snags) for two old-growth stands in the Valdivian Andes

	EAGB		Log		Snag		CWD	
Species	(Mg ha ⁻¹)	(%)	(Mg ha ⁻¹)	(%)	(Mg ha ⁻¹)	(%)	(Mg ha ⁻¹)	(%)
COMATE								
<i>N. dombeyi</i>	431	49	35	55	23	92	58	65
<i>L. philippiana</i>	149	17	5	7	0.9	4	5	6
<i>S. conspicua</i>	270	31	5	7	0.9	4	6	6
<i>D. diacanthoides</i>	27	3	-	-	-	-	-	-
Other sps.	0.7	0.1	20	31	0.1	0.2	20	22
Total	877	100	64	100	25	100	89	100
TEMATR								
<i>N. dombeyi</i>	-	-	2	3	0.6	10	2	4
<i>L. philippiana</i>	203	31	11	21	4	72	16	26
<i>S. conspicua</i>	262	39	14	25	0.8	14	14	24
<i>D. diacanthoides</i>	179	27	5	9	0.2	4	5	9
Other species	22	3	22	41	0.04	0.6	22	37
Total	666	100	54	100	6	100	59	100

3.5. Canopy gaps

There were more gaps of larger average size in the COMATE forest (Table V and Fig 3). The percentage of the transects that was intercepted by gaps in the COMATE forest accounted for 26%, more than double that in the TEMATR forest that was only 12%.

Table V. Number and general characteristics of gaps intercepted in each forest

Variable	COMATE	TEMATR
Length sampled (m)	2920	4000
Length intercepted (m)	755.7	478.4
% area intercepted by gaps	25.88	11.96
Number of gaps intercepted	40	31
Number of gaps in 1,000 m	13.69	7.75
Average length intercepted by each gap (m)	18.89	15.43

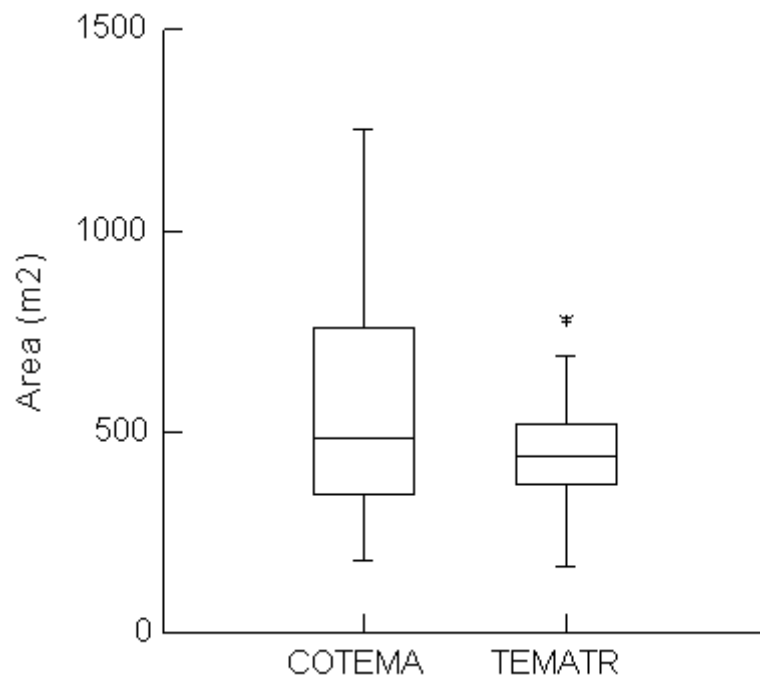


Fig. 3. Box plots representing the median, maximum and minimum gap sizes in each forest, in addition to the first and third quartiles and, in the case of TEMATR, an outlier corresponding to the larger gap

4. Discussion and Conclusion

There have been previous studies in the Valdivian Andes that show tree structure and composition. However, these studies have been focused on forest dynamics and especially the importance of large-scale disturbances in the regeneration of *Nothofagus* species. The current study adds a new perspective to the discussion on *Nothofagus* regeneration in this region. The differences in growth, tree composition and regeneration, and frequency and size of canopy gaps between the south aspect of the TEMATR forest with the north aspect of the COMATE forest suggest that in the former, protected from the winter storms, the smaller size and frequency of gaps in addition to the greater growth of *L. phillypiana* and *S. conspicua* (and likely most of the vegetation) make it difficult for the *N. dombeyi* regeneration to succeed.

This study also shows that the forest stand with emergent *Nothofagus* (COMATE) differs in its biomass, structure and composition from that lacking *Nothofagus* (TEMATR). The COMATE forest stand has greater biomass due to more basal area and a greater average height given by the presence of emergent *N. dombeyi* trees. The basal area of *N. dombeyi* in the COMATR forest is additive to that of the canopy species, and diameter growth of the more shade-tolerant species (*L. phillypiana*) independent from basal area of *N. dombeyi* [5]. This provides a great opportunity to optimise the biomass production of naturally-regenerated forests, and a clue to manipulate managed forest stands to increase its stratification for a greater productivity and biomass. Both stands have large trees that likely reach >400 (see Veblen 1985 for dbh-age relationships), and diameters between 200 and 300 cm.

Their structures resemble a reverse J shape, which in both forests is basically due to the diameter structure of *L. Philippiana*, but in the TEMATR forest the left tail is taller due to the great abundance of small-sized trees.

Overall, this study suggests that aspects may have a stronger influence on forest dynamics than it has been thought or reported before for this region [4]. Actually this subject has been usually neglected, probably because the Valdivian Andes corresponds to the Valdivian Temperate Rainforests and that has driven the idea that there are negligible effects of topography on forest growth and dynamics. The finding of different attributes in these forests should be considered when planning for their restoration, conservation or management. Foresters and ecologists should be aware that these differences could augment in the near future due to climate change observed during the last decades in the region [16].

Acknowledgements

This work has been supported by the Grant D-3497-1 from the International Foundation for Science to Pablo J. Donoso and Project FONDECYT N°1040169. We want to thank Daniel Soto, Daniel Uteau, Jan Bannister, Raúl Bertín, Rodrigo Vargas, Felipe Durán and Rick Sools for their hard work and patience to collect field data even under snow during the fall and winter of year 2004.

References

- [1] T.T. Veblen, F. Schlegel, and B. Escobar, „Structure and dynamics of old-growth *Nothofagus* forests in the Valdivian Andes”, *Journal of Ecology*, 68, 1-31, 1980.
- [2] T.T. Veblen, C. Donoso, F. M. Schlegel, and R. Escobar, “Forest dynamics in south central Chile”, *Journal of Biogeography*, 8, 211-257, 1981.
- [3] T.T. Veblen, “*Forest development in tree-fall gaps in the temperate rain forests of Chile*”, *National Geographic Research*, 1, 162-185, 1985.
- [4] C. Donoso, R. Deus, J. C. Cockbaine, and H. Castillo, “Variaciones estructurales del tipo forestal Coihue Raulí Tapa”, *Bosque*, 7(1), 17-35, 1986.
- [5] P.J. Donoso , and C. H. Lusk, C. H., “Differential effects of emergent *Nothofagus dombeyi* on growth and basal area of canopy species in an old-growth temperate rainforest”, *Journal of Vegetation Science*, 18, 675-684, 2007.
- [6] B.C. Schlegel, , and P. J. Donoso, „Effects of forest type and stand structure on coarse woody debris in old-growth rainforests in the Valdivian Andes, South-Central Chile”, *Forest Ecology and Management*, 255, 1906-1914, 2008.
- [7] M.P. Hernández , “Influencia de micrositios sobre la regeneración vegetal en bosques del tipo forestal Coihue-Raulí-Tapa de los Andes Valdivianos”, Tesis de Ingeniero Forestal, Universidad Austral, Valdivia, Chile, 2008.
- [8] C. Donoso, “Tipos forestales de los bosques nativos de Chile”, Documento de trabajo No 38, Investigación y Desarrollo Forestal (CONAF/PNUD-FAO) (Publicación FAO Chile), 1981.

- [9] P.J. Donoso, and C. Donoso, "Chile: Forest Species and Stand Types", Edited by: F.W. Cubbage. Society of American Foresters and International Society of Tropical Foresters, Accessed at: <http://forestryencyclopedia.jot.com/Wiki Home>, November 26, 2007.
- [10] P. Burschel, C. Gallegos, O. Martinez, and W. Moll, "*Composición y dinámica de un bosque virgen mixto de raulí y coigüe*", *Bosque* 1, 55-74, 1976.
- [11] C. Donoso, "Bosques templados de Chile y Argentina. Variación, estructura y dinámica", Editorial Universitaria, 1993.
- [12] T. Veblen, and D. H. Ashton, "Catastrophic influences in the vegetation of the Valdivian Andes", *Vegetatio*, 36, 149-167, 1978.
- [13] T.T. Veblen, "Nothofagus regeneration in tree-fall gaps in northern Patagonia", *Canadian Journal Forest Research*, 19, 365-371, 1989.
- [14] F.H. Borman, and G. E. Likens, "*Pattern and Process in a Forested Ecosystem*", Springer-Verlag, New York, 1979.
- [15] J. Tosso, "*Suelos volcánicos de Chile*", Instituto de Investigaciones Agropecuarias, INIA, Santiago, 1985.
- [16] R. Villalba, M. H. Masiokas, T. Kitzberger, and J. A. Boninsegna, "Biogeographical consequences of recent Climate Change in the Southern Andes of Argentina", in U.M. Huber, H.K.M. Bugmann, M.A. Reasoner (eds) *Global Change and Mountain Regions: An Overview of Current Knowledge*. Springer, the Netherland, pp. 145-157, 2005.

Leaf litter dynamics in a forested small Andean catchment, northern Patagonia, Argentina

Ricardo Albariño¹, Verónica Díaz Villanueva², Leonardo Buria³

¹Laboratorio de Limnología, INIBIOMA (Instituto de Biodiversidad y Medio Ambiente), CONICET Universidad Nacional del Comahue, 8400 Bariloche, Argentina, E-mail: ralbarin@crub.uncoma.edu.ar

²Laboratorio de Limnología, INIBIOMA (Instituto de Biodiversidad y Medio Ambiente), CONICET Universidad Nacional del Comahue, 8400 Bariloche, Argentina, E-mail: vdiaz@crub.uncoma.edu.ar

³Delegación Técnica Patagonia, Administración Nacional de Parques Nacionales, Gobierno de la República Argentina, 8400 Bariloche, Argentina, E-mail: lburia@apn.gov.ar

Abstract. This study describes structural and functional aspects associated with detritus dynamics in a *Nothofagus pumilio* forest small watershed that is located in the driest extreme of the eastwardly pluvial gradient in northern Patagonia. During the study the bulk of organic matter fell between late-summer and late-autumn (stream inputs of deciduous *Nothofagus* leaves collected in a neighbor stream = 97-111 g AFDM m⁻²). Leaf litter retained in the stream bottom was higher in autumn and winter (5-30 g DM m⁻²) and was dominated year round by *Nothofagus pumilio* (lenga). Detritus accumulations had 5 to 26 times more lenga leaves than those of other species. In the water year 2006, leaf litter shed at the driest period was redistributed along headwater extensions during the first spate (May 2006). In this event, a substantial amount of lenga leaves were exported from the upper catchment and travelled more than 9 km downstream. The average of our estimated *k* values (0.0067 ± 0.0017 , mean ± 1 s.e.) was at the lower limit of the intermediate decay rate category. Although lenga leaves seem to be of poor food quality and they dominate the benthic detrital food base in headwater streams most of the time, the community structure was dominated by detritivores (~75%) both in biomass and density with shredders representing ~50% of total biomass year round and collectors with ~50% of community density. Waterfalls act as natural physical barriers preventing the upstream settlement of the exotic rainbow trout and, in doing so, allow pristine functional and structural conditions to occur as in pre-trout introduction times.

1. Introduction

Streams are open and unidirectional systems where nutrient and matter exchanges with the surrounding landscape and downstream exportations are important ecosystem processes [1,2,3]. Allochthonous organic matter, mostly leaf litter, is a major source of food and refuge for aquatic invertebrates in low order temperate forested streams [4,5]. Although a large amount of fallen leaves is quickly transported downstream [6], a substantial quantity is retained in pools or by stones

and wood. Consequently, leaf litter lixiviates and becomes rapidly colonized by microbes and gradually by invertebrates that feed on it resulting in nutrient cycling and in the transference of matter and energy up in the food web [7]. Although a more constant temperature regime and the independence of humidity in a water environment distinguishes detritus decay from soil systems [8], water temperature and velocity (i.e. abrasive action) strongly affect the process [9,10]. In addition, water chemistry influences breakdown rates, and dissolved inorganic nitrogen and phosphorous are known to accelerate detritus decay [11]. The invertebrates inhabiting leaf litter accumulations are mainly detritivores belonging to the shredder and gathering-collector functional feeding groups (FFGs) [12] and both groups are predicted to coexist in temperate forested headwaters [2]. The biological processes involved in leaf litter breakdown in a stream patch may account for 70% of mass loss [13] where shredder feeding represents a significant part of this phenomenon [12,15,16].

The headwaters of the Pacific and Atlantic basins extending on both sides of the Cordillera de los Andes in northern Patagonia (39°S and 42°S) are canopied mostly by species of *Nothofagus* representing the most important source of organic matter to the watersheds. The genus *Nothofagus* is endemic to the Southern Hemisphere [17] and deciduous species are restricted to South America with six tree species. Among these, *Nothofagus pumilio* (Poepp. & Endl.) Krasser (the Patagonian mountain beech) has the broadest distribution, from 39° to 55° S forming a low temperature tree line at higher elevations [18], a feature indicated as distinctive of the South Andes [19]. Wildfires, deforestation, and silvicultural management have affected the uppermost forests on both sides of the Andes. Agricultural livestock industry in the central valley of Chile has intensified the rates of inorganic N release to the environment [20]. Airborne pollution from those human activities (e.g. nitrate, ammonium) is known to be spread by wind and to be deposited by rain and mist far away from its origin ultimately reaching watercourses. However, the chemistry of precipitation and inorganic N concentrations in running waters of the Andes range still reflect a close approximation to pre-industrial conditions [20,21,22]. One of the most direct impacts happening in those systems comes from the introduction of exotic fish. Salmonids from the Northern Hemisphere have been stocked in Patagonian freshwaters since early in the 20th century and little is known yet on the ecological effects going on in those ecosystems [23,24].

Dominant westerly winds from the Pacific determine a sharp precipitation gradient that characterizes ecological conditions in most of Patagonia determining vegetation distribution and hydrological regimes from mesic to xeric conditions [25]. Interannual climate variation is affected by ENSO (El Niño/Southern Oscillation) phenomena that determine heavy precipitation in El Niño years and dry weather in La Niña events [26]. Although the Andes range has a rain-shadow effect strongly reducing precipitation on its eastern side, interannual variability associated to ENSO is marked [25].

This study describes structural and functional aspects associated with detritus dynamics in a forested small catchment located in the eastern extreme of the pluvial gradient in northern Patagonia. It summarizes a series of studies in order to serve as a baseline for future research and comparisons with other pristine Chilean and Argentinean streams along the precipitation gradient, with other systems affected by human development or with those of other regions in temperate areas of the world.

2. Study Area

Studies were carried out in the Ñireco catchment belonging to the Nahuel Huapi Lake basin (41° 13' S; 71° 20' W). Ñireco stream has a total stream length of 20 km from its headwaters (2000 m a.s.l.) to the mouth at Nahuel Huapi Lake (760 m a.s.l.) and it drains 97 km² at the ecotone between the temperate forest and the steppe. Annual precipitations span 2000 to 1200 mm yr⁻¹ in the upper and lower fluvial extensions, respectively [27]. Discharge has a bimodal pattern with two peaks occurring in the rainy (fall-winter) and snowmelt (late spring) periods [25]. The lowest discharges correspond to April, determining the beginning of the Water Year (*sensu* Gordon et al. [28]).

The catchment is formed by an upper mountainous (74 km²) and a lower piedmont drainage area (apart of the upper watershed surface it drains 23 km²). The upper part is conformed by the Ñireco stream and its main tributary, the Challhuaco stream (Fig. 1). Fluvial geomorphology and steep slopes characterize the landscape. Channel configuration alternates interspersed step-pool reaches with a pool-riffle structure. Soon after the Challhuaco stream joins Ñireco, the stream leaves the forested area and runs through a lower and drier valley. Glacial and fluvial forces have modelled the lower catchment [29] and it presents a mixture of moraines and alluvial terraces, with wide channel width, smooth slopes, and morphology determined by run-riffle pool habitats, with bare or vegetated bars along the channel; the last 3 km runs through S.C. de Bariloche city [30].

Vegetation in the study area represents the xeric eastern border of the temperate rain forests shared between Chile and Argentina. A pristine deciduous forest of *N. pumilio* covers the upper belt of the watershed, up to the timberline. Human activity above 1100 m a.s.l. is restricted to hiking. Riparian vegetation gradually changes downstream towards a mixed tree-shrub physiognomy dominated by *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri, *Discaria* sp., *Diostea juncea* (Gillies & Hook.) Miers, *Lomatia hirsuta* (Lam.) Diels ex J. F. Macbr., *Nothofagus antarctica* (Forest.) Oerst., *N. pumilio*, *Schinus patagonica* (Phil.) I.M. Johnst. After entering the piedmont, exotic plants also add to the riparian strips and the final 5 km are mostly dominated by *Salix fragilis* L.

In the upper catchment, tributary streams are small and medium size courses with narrow (0-5 m) width and heavy shading produced by *N. pumilio* trees. In contrast,

the main stream channel forming the lower extension of the system has a 8-15 m width and the riparian vegetation does not provide important shading to the bottom. Fish has a settled population of rainbow trout *Oncorhynchus mykiss* (Walbaum); however the small high altitude surveyed streams: A1 and Refugio (in its upper extension) (see details below) have no fish at all as the presence of waterfalls avoids upstream trout migration (R. Albariño and L. Buria, unpublished data).

Volcanic and plutonic igneous rocks compose the parental material and determine the chemical nature of stream waters [21,31] with circum-neutral pH, low conductivity ($30\text{-}60\ \mu\text{S cm}^{-1}$), and low nutrient concentrations (N-NO_3 : $5\text{-}15\ \mu\text{g L}^{-1}$; P-PO_4 : $1\text{-}5\ \mu\text{g L}^{-1}$) [32]. Streambed roughness is determined by a dominance of cobble-boulder substrates additionally characterized in the mountainous valley by large wood logs. In the lower extension, the channel also has a cobble-boulder structure but finer sediment patches may occasionally be present (sand, gravel and pebble).

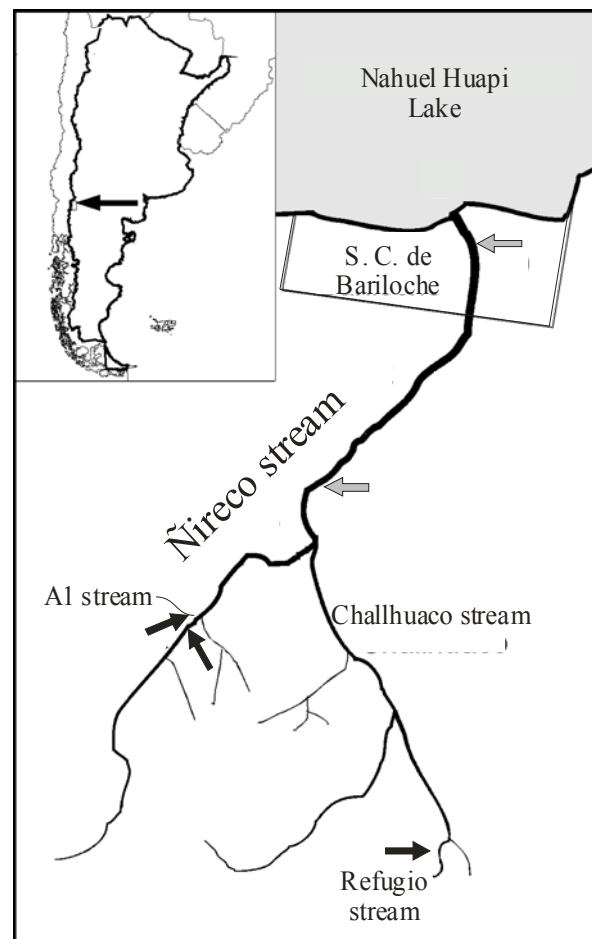


Fig. 1. Ñireco catchment. The lower valley begins after the Ñireco stream receives the Challhuaco stream. Black arrows indicate sampling and experimental sites at A1, Refugio, and Ñireco streams. Gray arrows indicate sampling sites at the beginning and end points of the lower extension of the Ñireco stream where drift samples were taken.

3. Material and Methods

3.1. Leaf litter Inputs, Retention and Exportation

Leaf litter input estimations are unavailable for the Ñireco catchment. We provide here information on allochthonous organic matter inputs quantified in an annual basis in the riparian zones of two small streams (R. Albariño, unpublished data) belonging to the Meliquina River catchment. The latter is located 80 km north of the Ñireco catchment but it also delimits the eastern distribution of the temperate native forest. Therefore, both catchments (named herein Capilla and Afluente Catedral) had originally similar vegetation characteristics and climatic conditions, but 35% of the Capilla watershed is afforested with *Pinus ponderosa* (Dougl.) Laws and *Pinus radiata* (D. Don). Five plastic collectors (individual surface: 0.12 m²) were placed on the forest floor near the stream channel during 2004-2005 and organic detritus was collected in six dates spanning 320 days. Collectors were placed in the upper bank to avoid being washed out by occasional spates. Detritus was classified in three main categories: leaf litter (entire leaves and identifiable fragments usually larger than 5 mm), woody debris (wood chunks, bark, twigs, seeds, buds), and others (including fine particulate organic matter: FPOM and flowers). Leaf litter was additionally classified in: deciduous, evergreen and pine needles. Afterwards, the different fractions of detritus were dried at 80°C for 48 h and weighed to the nearest 0.01g to obtain dry mass. This sampling procedure served as a reference to estimate allochthonous plant material inputs and its composition into streams but does not provide absolute quantification, as lateral inputs related to runoff may also be important.

During the beginning of the water year 2006, coarse particulate organic matter in transport (transported-CPOM) was measured at two sites of the Ñireco catchment. The sites were defined to estimate total exportation from the upper catchment and total exportation from the lower catchment (Fig. 1). Drift samples were collected at both sites with a D-frame net (n=3, 200 µm mesh size) at different dates in order to cover the period when the first spate in the water year 2006 occurred. Thus, pre-spate (baseline discharge), spate and post-spate drift samples were collected. Water volume filtered by the net for each sample was calculated by multiplying the net surface by mean water velocity measured with a digital flowmeter (Global Water, California, USA). Transported-CPOM was processed as already described and converted in g DM m⁻³. In this opportunity, only lenga leaves were sorted and weighed separately and the remaining fraction (i.e. other leaves and woody material) was also quantified to express total CPOM in the drift.

Retention was assessed by a semi-quantitative method, which consisted in obtaining a photographic record of the stream channel to identify leaf litter accumulations before and after the first spate in the 2006 water year. In a 50 m stream reach, ten

pictures were taken with an Olympus camera and height, width and length of the litter accumulations were registered.

3.2. Benthic Sampling: Detritus and Invertebrates

Benthic samples were taken from the stream bottom with a Surber sampler (0.09 m², 200 µm mesh size) to quantify and characterize benthic detritus and invertebrate community. Sampling was performed seasonally in July (winter) and November (spring) 1996, January (summer) and April (autumn) 1997 in a first order unnamed stream (denominated herein A1 stream, Fig. 1). Five replicates were taken at each sampling date and samples fixed in situ with 5% formalin. In a next survey, samples were taken monthly from March 2003 to February 2004 in a second order unnamed stream (denominated herein Refugio stream, Fig. 1) following the same procedure as described above. Samples from the 2003-2004 survey were pooled by seasons for comparative purposes.

In the laboratory, organic matter and invertebrates were fractioned by sieves and sorted. Detritus was classified in three main categories: leaf litter (entire leaves or fragments larger than 5mm), woody debris (wood chunks, bark, twigs, seeds, buds), and fine particulate organic matter (FPOM). Fine POM represents the detrital fraction between 1 mm and 200 µm, as the later was the mesh size used in the sampler. For the purposes of the paper only leaf litter and FPOM standing stocks are shown. Besides, leaf litter from the 1996-1997 survey was further assorted in two categories: lenga leaves and other leaves. Finally, particulate organic matter (POM) was dried, weighed and converted to g DM m⁻² as described above.

Taxa were identified, counted, placed in separate containers, dried at 80°C for 48 h and weighed to the nearest 0.0001g with an analytical balance. Invertebrates were assigned to their FFG *sensu* Cummins and Merritt [33] following available information in local and regional studies [34,35,36,37,38,39,40]. When specific studies on feeding ecology were unavailable, we performed gut content analysis and mouthparts morphology observations, complemented with bibliography from the Southern Hemisphere [41] to assign taxa to a FFG. Detritus and invertebrates were expressed as g DM m⁻² or number of individuals m⁻².

3.3. Breakdown of benthic leaf litter

Leaf litter bag experiments were performed to measure leaf litter decomposition. Two of the experiments were run in autumn-winter and two in spring-summer. The basic experimental design was similar but differences in stream size, experiment duration, mesh sizes, number of bags and initial leaf DM in litter bags are shown in Table I. One of the experiments was designed to compare breakdown rates between lenga leaves and *P. ponderosa* needles. This experiment was run in the main channel of the Ñireco stream (Fig. 1). The remaining experiments were designed to assess the effect of shredding invertebrates on lenga leaves mass loss in the A1

stream (spring-summer 1996-1997) and in the Refugio stream (spring-summer 2005-2006 and autumn-winter 2007) (Fig. 1).

Litter bags had a 18 x 12 cm size. Coarse mesh bags 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 [42]. Thus, it was assumed that large invertebrates could gain access to leaves and also that leaf fragments (>1 mm) produced by 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 invertebrate activities. The experiments where we used fine mesh bags had 1.0 mm (spring-summer 1996-1997) and 0.5 mm mesh size (autumn-winter 2007). 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 at senescence of lenga leaves. Leaf litter bags were placed in run-riffle areas along 80 m reaches on each stream. Five litter bags per treatment (three replicates per treatment in the autumn-winter experiment at Refugio stream) were collected at different times of exposure and returned to the laboratory where remaining leaf litter was gently washed and invertebrates removed. Remaining leaf litter was processed as described above to obtain g DM per bag. Decay rate was estimated by linear regression of the natural logarithm of remaining leaf DM on days of exposure assuming an exponential decay model [14]. In the 1995-1997 experiments cumulated degree-days were calculated by multiplying mean water temperature at different intervals by total days in the interval along the experimental period. In the 2005-2007 experiments, cumulated degree-days were obtained by summing the daily mean temperature registered by a datalogger (Onset Computer Co., Maine, USA) datalogger along the experimental period.

3.4. Statistical Analysis

We compared breakdown rates between treatments in the different litter bag experiments by one-way ANCOVAs on the natural logarithm of leaf litter mass remaining in bags using days as covariate [43]. The same procedure was used to test for differences in decay rates between spring-summer and autumn-winter experiments. In this analysis, we compared the ANCOVA outputs by running separately the analyses using days or cumulated-degree days as covariate.

4. Results

4.1. Particulate organic matter inputs

During the study the bulk of organic matter fell between late-summer and late-autumn (Fig. 2). In the Afluente Catedral stream, it was mostly composed by deciduous leaves (97-111 g AFDM m⁻²) and woody material. From early-winter to

late-spring woody material dominated the detrital inputs, probably associated with snow and wind periods. Evergreen leaves represented a small proportion of allochthonous detritus belonging to riparian shrubs. Reproductive structures (bud scales, flowers) and FPOM, both included in the category *others* peaked in autumn (FPOM) and early summer (reproductive structures). In contrast, in the partially afforested watershed, Capilla stream, pine needles dominated the composition of POM year round and deciduous leaves (from *N. pumilio* and *N. antarctica*) were the next category of importance.

4.2. Benthic Particulate Organic Matter in erosional habitats

Benthic POM in two small streams tributaries of the Ñireco stream varied seasonally (Fig. 3). Leaf litter retained in the stream bottom was higher in autumn and winter (5-30 g DM m⁻²), reflecting input timing of deciduous leaf species dominant in the catchments. The nature of the dominant tree *Nothofagus pumilio* as the main source of allochthonous detritus to the stream ecosystem was observed year round in the benthic detritus standing stock (Fig. 4). Leaf litter accumulations in the A1 stream were dominated by lenga leaves being 5 to 26 times higher than those of accompanying riparian shrubs. Fine POM was less variable in both streams with a slight increase towards the driest period (summer). Overall, benthic POM was more abundant in the Refugio stream than in the A1 stream (Fig. 3), which may be explained by differences in annual weather conditions and in catchment and stream characteristics (catchment surface, stream discharge and retentiveness, forest density, etc.).

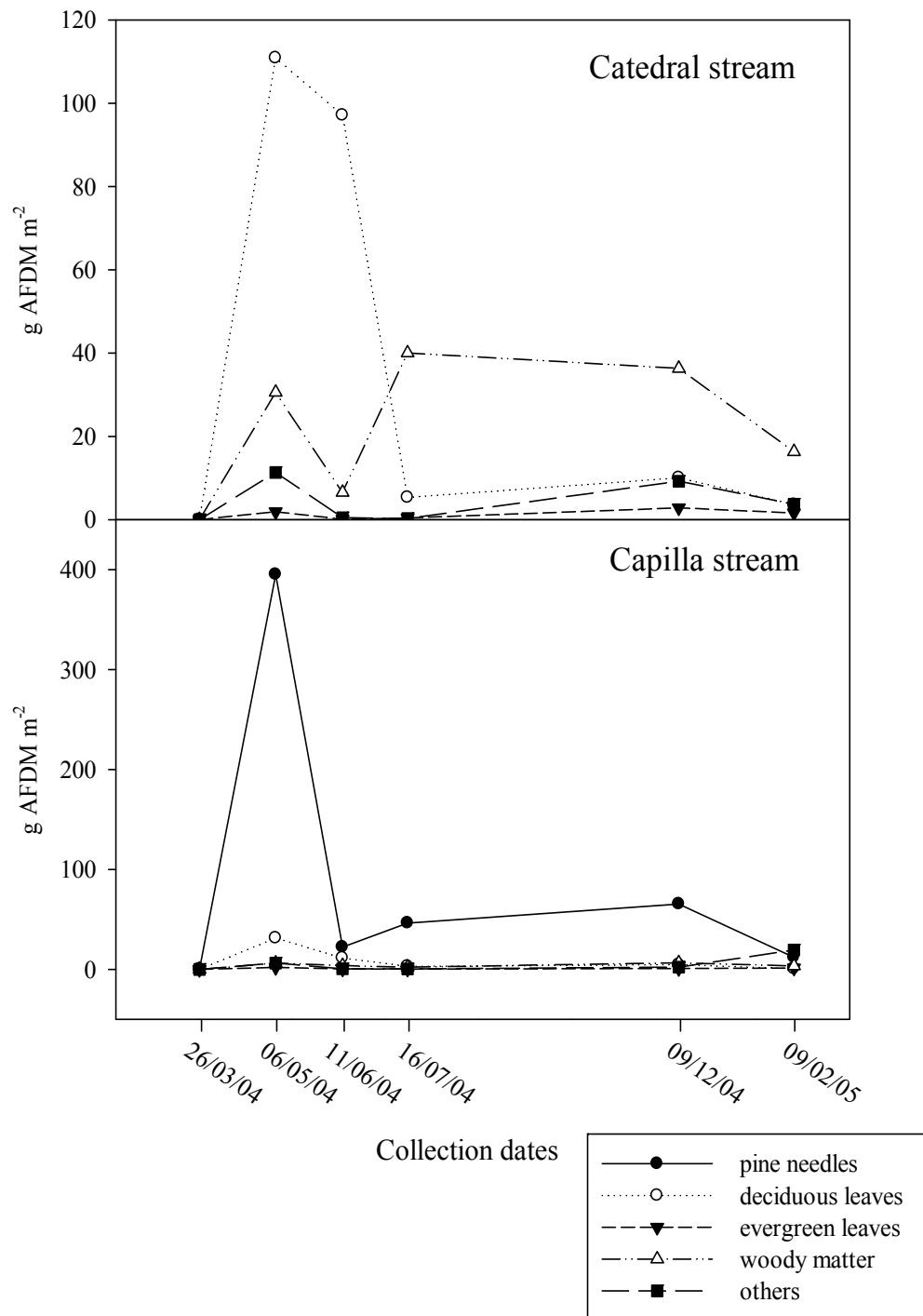


Fig. 2. Vertical inputs of particulate organic matter (POM) estimated leaf litter traps placed near the stream bank in two low order forested streams. Capilla stream is partially afforested with the exotic *Pinus ponderosa* (Dougl.) Laws and *P. radiata* (D. Don), which extended up to the stream margin at the study site. Thus, mass of pine needles was quantified separated from evergreen native species.

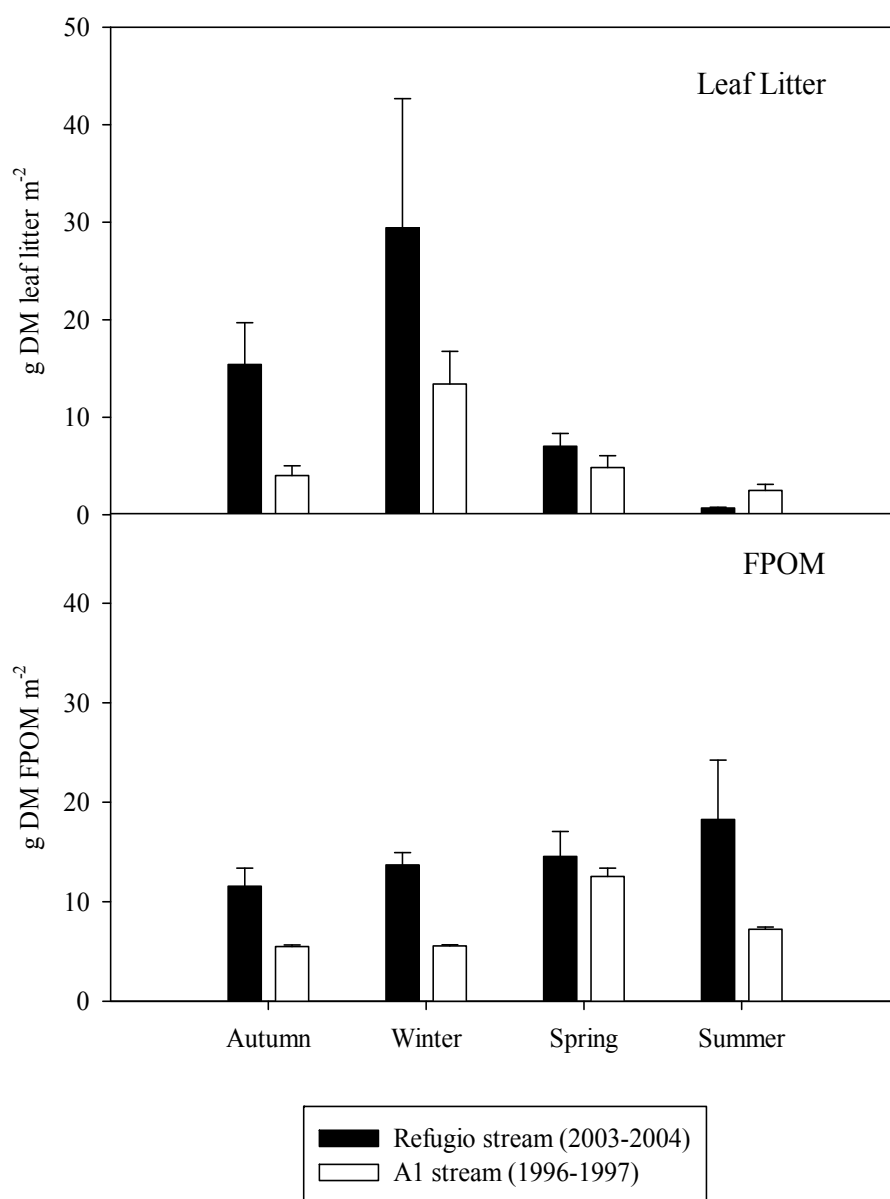


Fig. 3. Benthic POM standing stock from two small streams in the upper Ñireco catchment. Leaf litter and FPOM ($\geq 200\mu\text{m}$) from seasonal samplings in 1996-1997 and 2003-2004 are shown (mean \pm 1 s.e.)

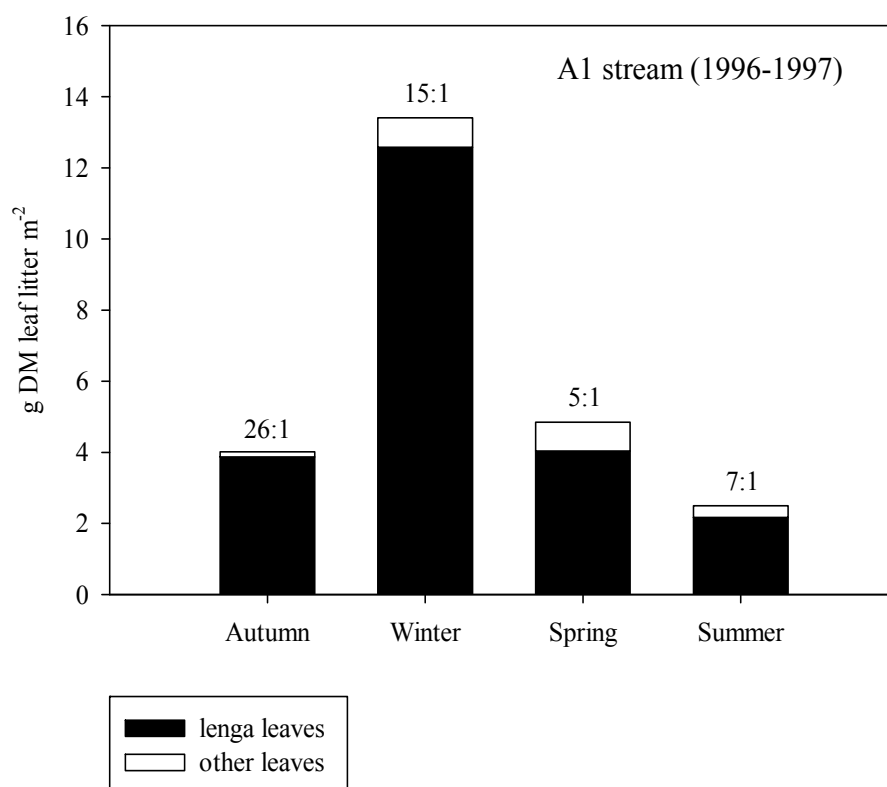


Fig. 4. Composition of leaf litter benthic accumulations in two categories: lenga (*Nothofagus pumilio*) and other leaves in the A1 stream (upper Ñireco catchment). Lenga is the only tree forming the upper forest belt. Numbers on top of bars show the lenga:other leaves ratio based on DM.

4.3. Stream retention and downstream exportation of leaf litter

During leaf litter shedding in March and April 2006, large wood logs and coarse inorganic substrates distributed along the bottom of the Refugio stream efficiently acted as physical retention devices. Boulders and cobble aggregations that protrude from the bottom surface retained floating and drifting leaves. These circumstances were associated by the lowest stream discharges registered in April 27 and May 19 (15.5 and 12.0 L s⁻¹, respectively) at Refugio stream. On May 19, large leaf litter accumulations (up to 1 m² and 30 cm depth) were observed along the channel. In many situations the accumulations extended laterally to reach the stream banks covering the whole channel section and increased in height to form a dam entirely from leaves (Fig. 5). The small size of lenga leaves (1-4cm) developed a structural pattern in which newly trapped leaves were arranged in layers upstream to the already retained leaves. By changing the hydrodynamic features of the channel, those dams became transient pool habitats, which favored the deposition of fine inorganic and organic sediments at the upstream adjacent zone.

The first heavy storm in the Water Year 2006 occurred in the area between May 15 and 17 (preceded by a light rain occurring on 27 April 2006). Although in this event, part of the precipitation in the upper catchment had been deposited as snow, water discharge measured at the beginning of the lower extension of the Ñireco stream (Fig. 1) raised from 320 (May 13) to 484 L s⁻¹ (May 15) (Fig. 6a). Concomitantly, a large portion of the stored leaf litter in the upper catchment was registered in transport (5 g DM fresh lenga leaves L⁻¹) to the downstream reach (Fig. 6b). After ten days, lenga leaves originated in the upper catchment were sampled in transport (3 g DM lenga leaves L⁻¹) at the site located near the Ñireco stream outlet (Fig. 1, 6c). Visual inspection of leaves in the laboratory showed that most of them were unconditioned (i.e. they had been recently entered the system). Thus, those leaves traveled more than 9 km. In addition, an inspection of the Refugio stream channel done on 27 June 2006 confirmed that large amounts of lenga leaf packs had already disappeared in relation to the precedent spate and the gradual increase in water discharge (Fig. 5). At that date, few small leaf litter patches (20 x 20 cm) were still trapped upstream of retention devices but most of the leaf litter was found within and underneath the inorganic substrate.

4.4. Aquatic Biota

The benthic community was dominated by larval stages of aquatic insects. Mean annual abundances were very similar in both streams: 3169 individuals and 2499 mg DM m⁻² in the Refugio stream and 3165 individuals and 1705 mg DM m⁻² in the A1 stream (Table II) with higher densities and lower total biomass registered during summer, as a consequence of the emergence of large specimens and the recruitment of new cohorts. The functional community structure was dominated by detritivores that were ~75% of total community abundance year round either in biomass or density. Coarse detritus feeders (or shredders) represented ~50% of total biomass

year round, and fine detritus feeders (collectors) represented ~50% of community density (Fig. 7). Grazers were more abundant in the Refugio stream suggesting that primary production occurring under the forest canopy also supported a fraction of that food web. In both streams, shredders were represented by eight species belonging to Diptera (2 tipulids: *Monophilus* sp., *Tipula* sp.), Plecoptera (1 austroperlid: *Klapopteryx kuscheli* Illies) and Trichoptera (2 sericostomatids: *Parasericostoma cristatum* Flint, *Myotrichia murina* Schmid and 2 limnephilids: *Austrocosmoecus* sp., *Monocosmoecus* sp.).



Fig. 5. Left: Large leaf pack of lenga leaves on a stream margin of the Refugio stream. Baseflow on May 19, 2006. On the left side of the photo the accumulation protrudes 15 cm into the channel narrowing its width. Leaf pack height is 22 cm and determines pool type conditions. Right: base flow on June 27, 2006. Retentive devices (stones, branches and snags) have lost their capacity of retaining leaf packs. At this time, leaf litter is redistributed in the stream channel within and underneath substrate interstices or exported to downstream reaches. In both photos the flow goes from right to left.

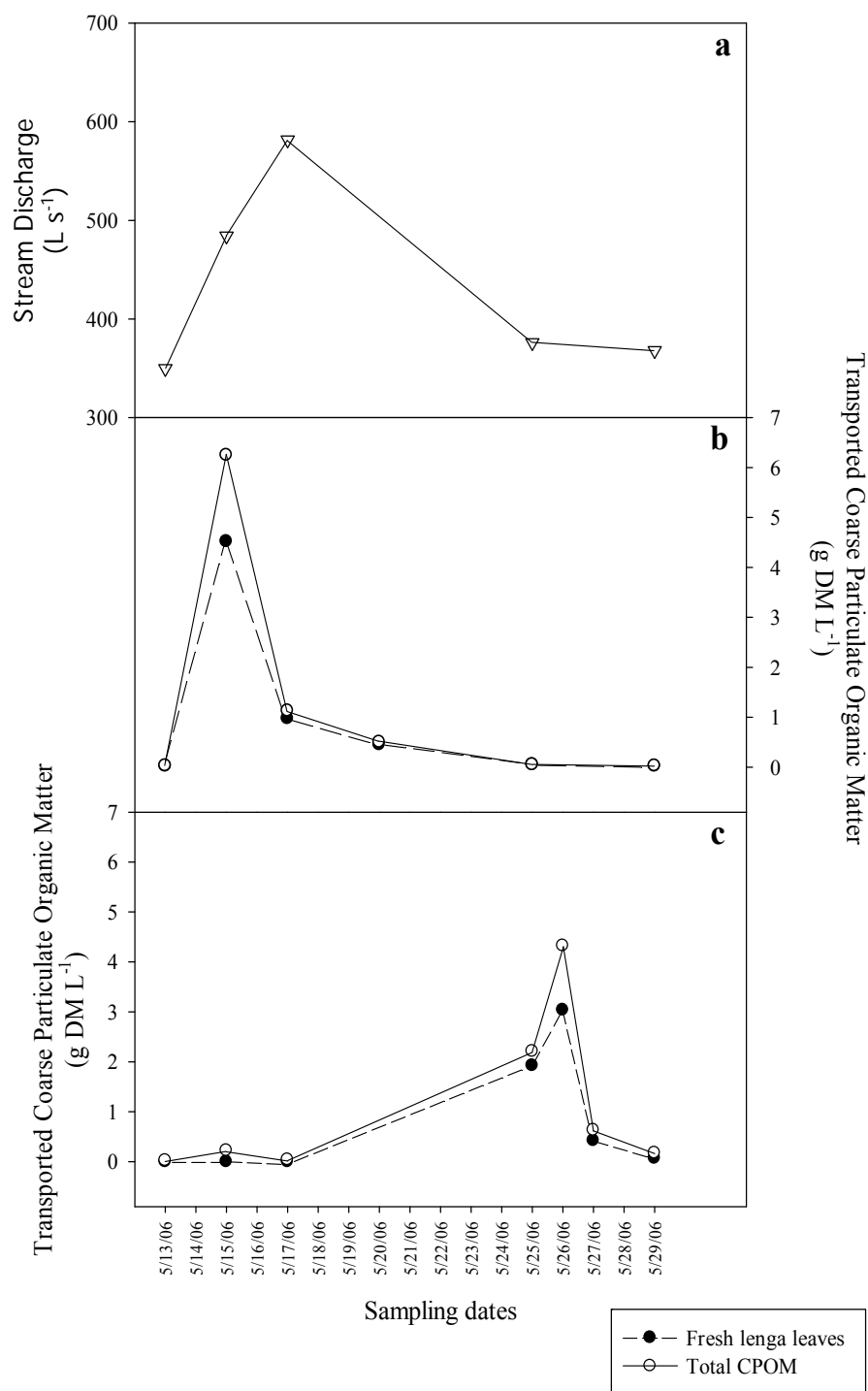


Fig. 6. a) Stream discharge measured at the beginning of the lower Ñireco catchment; b), c) transported CPOM measured at the beginning and at the end of the lower Ñireco catchment. Data were registered in the first pre- and post-spate event in the Water Year 2006. Stream discharge at the downstream end of the Ñireco stream was not measured for safety reasons. Sampling sites indicated by gray arrows in Fig. 1.

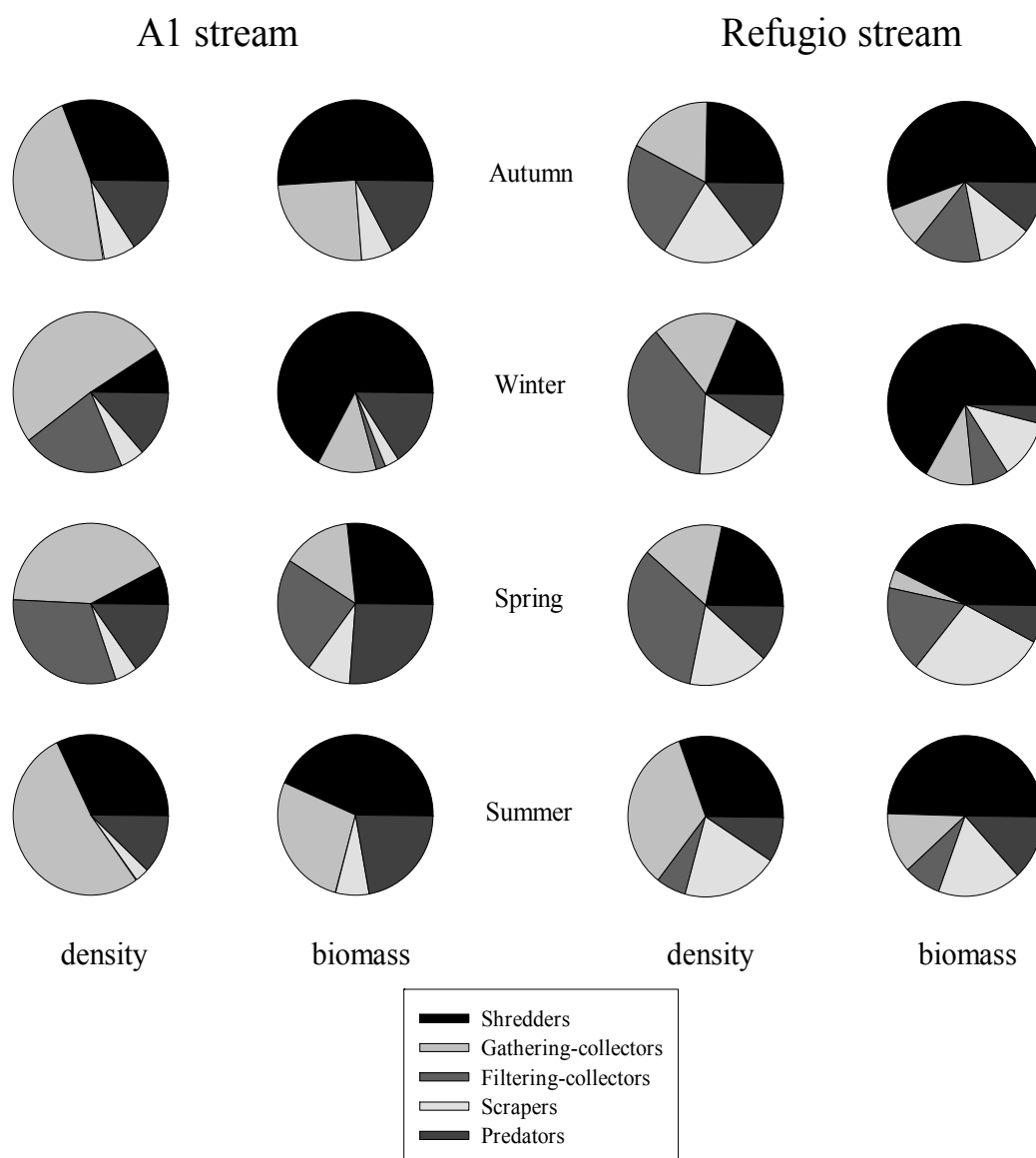


Fig. 7. Community functional structure of benthic invertebrates in two small streams at the upper catchment of the Ñireco stream; samples were taken seasonally in erosional habitats (riffles and runs)

Table I. Leaf litter bag experiment to assess litter breakdown in different streams within the Ñireco catchment. Water temperature refers to mean temperature during the experiment. Breakdown k rates and half-life times ($t_{50\%}$) were estimated using a single exponential decay model.

stream	stream size	water temperature (°C)	experimental design	leaf litter species	mesh size (mm)	season	experiment duration (days)	total n	initial litter DM (g)	treatment	breakdown rate (k)	$t_{50\%}$	ANCOVA summary	Source
A1	1st	8.7	coarse vs. fine mesh bags	<i>Nothofagus pumilio</i>	10 vs. 1	spring -summer 1996-1997	118	45	3.5	Coarse	0.0074	94	$F_{(1,48)} = 6.37$ $p = 0.014$	Albariño and Balserro 2002
Ñireco	3rd	3.4	lenga vs. pine	<i>N. pumilio</i> , <i>Pinus ponderosa</i>	10	autumn -winter 1995	135	40	4.0	Lenga	0.0033	212	$F_{(1,37)} = 9.66$ $p = 0.004$	Albariño and Balserro 2002
Refugio	2nd	7.4	coarse mesh bags	<i>N. pumilio</i>	10	spring -summer 2005-2006	135	25	2.0	Coarse	0.0113	61		Burta 2008
Refugio	2nd	1.9	coarse vs. fine mesh bags	<i>N. pumilio</i>	5 vs. 0.5	autumn -winter 2007	112	18	1.0	Coarse	0.0049	141	$F_{(1,21)} = 1.34$ $p = 0.260$	Albariño, unpublished
										Fine	0.0036	193		

Table II. Benthic community abundance of invertebrates in two small streams of the Nireco upper catchment

	Autumn		Winter		Spring		Summer	
	no. indiv. m ⁻²	mg DM m ⁻²	no. indiv. m ⁻²	mg DM m ⁻²	no. indiv. m ⁻²	mg DM m ⁻²	no. indiv. m ⁻²	mg DM m ⁻²
A1 stream								
(1996-1997 survey)								
Shredders	660	741	196	1225	281	452	1563	801
Gathering-collectors	981	369	1074	228	1478	237	2546	504
Filtering-collectors	6	1	453	36	1111	396	9	2
Scrapers	143	97	108	56	169	152	143	129
Predators	331	251	285	289	542	444	583	413
TOTAL	2119	1458	2115	1833	3581	1680	4844	1848
Refugio stream								
(2003-2004 survey)								
Shredders	668	1326	518	1904	705	1268	1223	875
Gathering-collectors	468	200	483	290	540	111	1342	215
Filtering-collectors	631	342	1042	219	1063	515	248	137
Scrapers	529	274	489	350	548	844	810	310
Predators	387	251	244	106	371	227	366	235
TOTAL	2681	2393	2777	2869	3229	2964	3989	1773

4.5. Leaf Litter Processing

Shredding signs were observed in the remaining leaf material of coarse mesh bags, except in pine needles where only microbial colonization was noticeable after 112 d of being immersed in the stream. This observation was reflected in the significant lower breakdown rate estimated for pine needles compared to that of lenga leaves (Table I).

Breakdown rates of *N. pumilio* leaves exposed to invertebrate colonization (coarse mesh bags) were lower in autumn-winter (0.0033 and 0.0049) than in spring-summer experiments (0.0074 and 0.0113) (Table I). The difference was significant between cold and warm seasons when days were used as covariate (ANCOVA, $F_{1,79} = 7.20$, $P = 0.009$). However, when using cumulated-degree days as covariate, no difference was found between seasons (ANCOVA, $F_{1,79} = 1.81$, $P = 0.182$) indicating that water temperature was a key factor accelerating litter breakdown during warmer months. Water temperature in spring-summer experiments (7.4-8.7°C) was on average three times higher than that registered in autumn-winter experiments (1.9-3.4°C). Shredders had a significant effect on leaf litter decay in the A1 stream (spring-summer experiment) but did not in the autumn-winter experiment (Refugio stream) (Table I).

5. Discussion

The understanding of detritus dynamics in streams, its origin and fate, and how it affects ecosystem functioning and structure has already been gathered for more than 30 years [44]. Most of this research has been done in temperate biomes; within them, however, there are regions in the world where little evidence arises on patterns, mechanisms and their links with biotic components of such systems. The headwaters in the temperate forests of the Cordillera de los Andes in Patagonia represent one of those gaps.

The Ñireco catchment is a mountainous small fluvial network located at the eastern drier distribution of those forests where ecological processes connect both terrestrial-aquatic systems and upper-lower extensions within the valley. In our study, the bulk of leaf litter entered the systems in the late summer-autumn period when flows are the lowest and it was temporally retained *in situ*, providing substrate, nutrients, and food for microbes and invertebrates [42]. Detritus input from riparian vegetation makes up most of the standing stock of organic material in small temperate forested streams [45], and invertebrate detritivores in such streams feed largely on this allochthonous material [12,46,47]. As a consequence of breakdown, the energy of dead plant material enters the food web to support higher trophic levels within the same system or returns to the terrestrial environment when

adults leave the stream to reproduce and disperse [48]. Secondly, at the time of the first spates large amounts of lenga leaves were exported more than 10 km downstream within the fluvial continuum representing a net subsidy for spatially distant food webs. Exportation of detritus is a common process in running waters that link ecologically different extensions along the longitudinal axes [1,49], particularly associated to high discharge events and retention capacity of streams [50]. In our example, the piedmont lower extension of the Ñireco stream is wide and poorly influenced by riparian vegetation shading. Primary producers on inorganic substrates are likely to support most of the food web. Our results point out that leaf litter, a temporal substantial resource, derived from upslope might play an important role on the functioning of this extension.

5.1. The ecological relevance of *Nothofagus pumilio* to streams

The mountain beech *Nothofagus pumilio* densely covers the upper catchments of the Patagonian Andes both in latitudinal and longitudinal dimensions. In the Nahuel Huapi National Park, where this study was done, it represents more than 46% of woodlands and it is the only tree species conforming the high-altitude forest. Therefore, in upper catchments the phenology of *N. pumilio* rules the quantity, quality and timing of allochthonous detritus supply to streams. The population dynamics of this species is also responsible for coarse woody debris inputs [51], which has important implications in the development of channel structure, habitat formation for aquatic insects and fish, and leaf litter retention [6,52] as shown for other *Nothofagus* species [53]. The present study highlights the importance of *N. pumilio* detritus as a basal energetic resource for Andean stream food webs. Most of the matter comes in the form of leaf litter and during late summer-autumn. However, during the species post-reproductive period (December-January), flowers and seeds fall into streams and may represent another transitory energetic resource (present study, data not shown). Snow and wind are meteorological factors also responsible for POM inputs to streams [1]. In particular, late springs are windy seasons in the region and broken branches with already mature grown leaves can be found in streams. Mature lenga leaves are likely a fresh food resource for detritivores at this time. In a laboratory experiment with pre-conditioned mature and senescent lenga leaves, larvae of the common South American shredder *K. kuscheli* preferred to feed on the mature ones (R. Albariño, unpublished). This is not surprising as mature *N. pumilio* leaves can have four times more % N and three times more % P than senescent leaves [54].

The nutrient-poor conditions of the Andean headwater streams seem to be related to parent material, forest-soil biogeochemistry, and low human development [21,31]. The forests are mainly N-limited, and N is significantly resorbed from senescent leaves resulting in a low N:C ratio in shed leaves [54]. As a result, lenga leaves seem to be of poor food quality that dominates the benthic detrital food base in headwater streams most of the time. The average of our estimated k values (considering only coarse mesh bag experiments, 0.0067 ± 0.0017 , mean ± 1 s.e.)

was at the lower limit of the intermediate decay rate category (for riparian leaf species = $0.005 > k > 0.010$, [14, 55]). Regarding the variability of the obtained rates it may be classified as a slow decaying species, as Petersen and Cummins [14] considered for the deciduous Fagaceae *Quercus alba* L., which showed a similar average. Breakdown rates in *Nothofagus* species have also been studied in New Zealand [56,57,58] indicating that leaf litter of those species fell into the slow decay category. However, a comparison with our estimated decay rates in *N. pumilio* leaves may be misleading, as *Nothofagus* New Zealand trees are evergreen.

Heterotrophic microbes growing on leaf litter are able to sequester inorganic dissolved N and P [59,60], enhancing conditioning and quality of leaf litter as food and subsequently fastening the decomposition process. Andean streams with low nutrient concentrations might have low microbial activity, and consequently slow microbial colonization and litter conditioning, which is probably declined by low autumn-winter temperatures [9]. However, in our experiments, lenga leaves were well conditioned after two months in the streams and prompted to be consumed by detritivores, as shredding signs were already observed. Although lenga leaves seem *per se* to be a low quality food resource [61], which take long to be conditioned, Albariño et al. [62] measured hyphomycetes biomass in lenga leaves after two months submerged in a nearby stream that was comparable to the average biomass measured on decaying leaves [63,64]. In addition, naturally conditioned lenga leaves offered under laboratory conditions and in field experiments to *K. kuscheli* produced larval growth [39,62].

Breakdown rates of *N. pumilio* leaves exposed to invertebrate colonization were lower in autumn-winter (0.0033 and 0.0049) than in spring-summer experiments (0.0074 and 0.0113), associated to the lower thermal regime of colder seasons slowing down detritus breakdown rates. However, when experiments were compared by normalizing the degree-days in both experiments (i.e. eliminating any effect of different thermal regimes), decay rates did not differ statistically, indicating that shredding activity was equally important in both seasons [9]. Interestingly, shredders had a significant effect on the leaf litter decay experiments conducted in spring-summer, but not in the autumn-winter experiment conducted in 2007 (Refugio stream), when shredder activity-coupling to leaf litter input timing should have been maximized. The plausible explanations to those findings are related to the field manipulation experiments. In 2007, the experiment coincided with a dry autumn-winter season allowing the storage of large amounts of leaf litter in the stream bottom for longer than usual (i.e. large leaf packs were present in October, R. Albariño, pers. obs.). Thus food was probably in excess relative to shredder abundance in the system and shredding activity within litter bags was undetectable. In contrast, summer seasons in dominated deciduous forest streams are expected to be periods of low food availability for shredders [65]. So, the introduction of small patches of food into the stream (i.e. leaf litter bags) would have represented isolated food microhabitats prone to rapid colonization and consumption by shredders [66,67].

It has been shown that removal of CPOM inputs to streams [5] and forest replacement by tree species with contrasting phenology (e.g. changed litterfall timing, poor physical and chemical leaf characteristics and slower breakdown rates) [68,69] affect stream functioning and their aquatic communities. Those findings have important implications in forestry ecology and conservation issues. In our experiments, we estimated that pine needles would take twice the time that lenga leaves to lose half of their mass, but differences in leaf shedding or in bottom retentiveness of the deciduous and evergreen species were not analyzed. In a similar leaf litter bag experimental design carried out in winter 1997 in a low order stream of the Bío Bío basin, central Chile, Valdovinos [70] compared decomposition and invertebrate colonization on *N. pumilio* leaves and *Pinus radiata* needles. He found that lenga leaves broke down twice faster than the exotic pine needles ($k = 0.0072$ vs. 0.0027) and the difference was associated to feeding activity of the shredder collected in the bags. Comparing the k breakdown rate for lenga between his study and those of our winter experiments, we observed that breakdown was slower in our streams. Water temperature might be the explanation, as his experiment was run within a temperature range of 6-14°C, what was three times the autumn-winter thermal regime registered in our streams. In a field manipulation at the Refugio stream (Albariño et al. unpublished), litter bags with alder leaves (*Alnus glutinosa* (L.) Gaertn.), a species known to have high-quality leaves as food [71], were attached to the bottom during the lenga litter fall period. After 28 days, leaf packs were found colonized by shredders and leaves had conspicuous feeding signs, indicating that those coarse-particle feeders were able to detect small food patches of high quality in a habitat which, at that time, was stored up with large amounts of low-quality food (i.e. unconditioned lenga leaf litter).

5.2. The community of consumers

As in many other headwaters of the world, benthic invertebrates represent the dominant fraction of consumers [72,73,74]. Aquatic insects, mostly dipteran, plecopteran, ephemeropteran and trichopteran species, dominated the assemblages. Many of them are endemic at species to family level [75,76,77,78]. Functional feeding groups were dominated by detritivores year round as in other temperate small forested streams in Patagonia [37], Europe [79,80,81] and North America [2,82]. Gathering-collectors and filtering-collectors were the most important in terms of abundance, and shredders dominated the assemblages, in terms of biomass. The shredder FFG was formed by a small set of species, which are common species in other small streams of the region. However, the large shredders belonging to the genus *Diamphipnoa* and *Diamphipnopsis* were not present in the catchment. Those shredders seem to have a distribution more correlated with a mesic temperate forest as they are well distributed in Chilean small streams [83,78] and they are also present in Argentinean streams draining into the Pacific basin [84,85].

Although primary producers are constrained to shade-tolerant species, they may support a substantial fraction of grazers (V. Díaz Villanueva, unpublished). The patterns of benthic invertebrate FFG abundances varied seasonally. Although total invertebrate density and biomass were similar in both streams, or at least in the same order of magnitude, some FFG abundances differed. The higher numbers of filtering-collectors and scrapers in the Refugio stream were likely associated to the stream size (second order in the Refugio stream and first order in the A1 stream) which, in combination with forest dynamics (i.e. tree falling-open gaps), likely allowed sunlight entrance and substantial primary production. Shredders showed a pattern associated with that of leaf litter availability into the streams.

6. Conclusions

The role that headwaters play within fluvial networks has been re-emphasized in recent syntheses [3,86]. Small forested streams in the Andes of Patagonia provide abundant retention devices for allochthonous leaf litter until spates occurring in late autumn-early winter (rainy season) serve to redistribute leaf litter along headwater extensions. In addition those spates remove and transport a substantial amount of OM subsidizing the biota and favoring heterotrophic processing along downstream more open reaches.

A representative area of the major basins of the Atlantic slopes in Patagonia is under the protection of the Administration of National Parks, Argentina. In this regard, water and catchment issues that may threat biodiversity and ecological integrity of those fluvial systems are still sparse or are mostly associated to human settlements (i.e. urbanization, forestry, water subtraction, crops and cattle raising, tourism). Perhaps the most widespread threat is the ongoing dispersion of the invasive brown and rainbow trout. Buria et al. [87] have recently shown that rainbow trout, which is the exotic fish more commonly found in smaller streams, alters the invertebrate community structure by affecting total body size spectrum and the relative abundance in biomass of the FFGs. There is also evidence that rainbow trout predation cascade down altering detritus breakdown and benthic algal accrual [88] as it has been demonstrated in New Zealand streams [89,90]. This conservation issue conflicts with the importance of such sportive fishery that represents a recreational and economical benefit. Waterfalls that act as natural physical barriers prevent the upstream settlement of trout and, in doing so, allow pristine functional and structural conditions to occur as in pre-trout introduction times. From the fishery viewpoint, small watersheds supply aquatic insects, which are exported in the drift, nurturing trout populations inhabiting downstream extensions [91].

Interannual climatic variation strongly affects the patterns and mechanisms of detritus dynamics [28]. The differences in leaf litter inputs, retention and breakdown, and exportation between wet and dry years need more research in order

to quantify how seasonal climate variation changes detritus decay patterns and the extent of these effects on benthic communities, particularly those of invertebrates at the level of populations and communities.

Acknowledgments

We thank the landowners of Estancia San Jorge, Meliquina, Neuquén for allowing us access to their property. Permits to carry out the study in the Nahuel Huapi National Park, Argentina were obtained at the Technical Agency of the National Park Administration. This work was supported by the CONICET (Grant #PIP 112-200801-01702) and FONCYT (Grant #PICT-2007-01747).

References

- [1] S.G. Fisher, and G.E. Likens, "Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism" *Ecological Monographs*, 43, 421-439, 1973.
- [2] R.L. Vannote, G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing, "The river continuum concept" *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130-137, 1980.
- [3] T. Gomi, R.C. Sidle, and J.S. Richardson, "Headwater and channel network - understanding processes and downstream linkages of headwater systems" *BioScience*, 52, 905-916, 2002.
- [4] L. Rowe, and J.S. Richardson, "Community responses to experimental food depletion: resource tracking by stream invertebrates" *Oecologia*, 129, 473-480, 2001.
- [5] J.B. Wallace, S.L. Eggert, J.L. Meyer, and J.R. Webster, "Effects of resource limitation on a detrital-based ecosystem" *Ecological Monographs*, 69, 409-442, 1999.
- [6] J.R. Webster, E.F. Benfield, T.P. Ehrman, M.A. Schaeffer, J.L. Tank, J.J. Hutchens, and D.J. D'Angelo, "What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta" *Freshwater Biology*, 41, 687-705, 1999.
- [7] R.O. Hall, J.B. Wallace, and S.L. Eggert "Organic matter flow in stream food webs with reduced detrital resource base" *Ecology*, 81(12), 3445-3463, 2000.
- [8] R.W. Merritt, and D.L. Lawson, "The role of leaf litter macroinvertebrates in stream-floodplain dynamics" *Hydrobiologia*, 248, 65-77, 1992.
- [9] J.G. Irons, M.W. Oswood, R.J. Stout, and C.M. Pringle, "Latitudinal patterns in leaf litter breakdown: is temperature really important?" *Freshwater Biology*, 32, 401-411, 1994.
- [10] V. Ferreira, M.A.S. Graça, L.M.P. de Lima João, and R. Gomes, "Role of physical fragmentation and invertebrate activity in the breakdown rate of leaves" *Archiv für Hydrobiologie*, 165, 4, 493-513, 2006.
- [11] Suberkropp, K. and E. Chauvet, "Regulation of leaf breakdown by fungi in streams: influences of water chemistry" *Ecology*, 76, 1433-1445, 1995.

- [12] K.W. Cummins, M.A. Wilzbach, D.M. Gates, J.B. Perry, and W.B. Taliaferro, "Shredders and riparian vegetation" *BioScience*, 39, 24-30, 1989.
- [13] K.W. Cummins, "Invertebrates", 75-91, in G. Petts, and P. Calow (eds.) *River biota*, Blackwell Science, Oxford, 1996.
- [14] R.C. Petersen, and K.W. Cummins, "Leaf processing in a woodland stream" *Freshwater Biology*, 4, 343-368, 1974.
- [15] T.F. Cuffney, J.B. Wallace, and G.L. Lugthart, "Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams" *Freshwater Biology*, 23, 281-299, 1990.
- [16] C.T. Robinson, M.O. Gessner, and J.V. Ward, "Leaf breakdown and associated macroinvertebrates in alpine glacial streams" *Freshwater Biology*, 40, 215-228, 1998.
- [17] H.H. Allan, "Flora of New Zealand", vol. 1, Manaaki Whenua Press, Wellington, 1982.
- [18] R. Hildebrand-Vogel, R. Godoy, and A. Vogel, "Subantarctic-Andean *Nothofagus pumilio* forests. Distribution area and systematic overview, vegetation and soils as demonstrated by an example of a South Chilean stand" *Vegetatio*, 89, 55-68, 1990.
- [19] P. Wardle, "Comparison of alpine timberline in New Zealand and the Southern Andes", Royal Society New Zealand, Miscellaneous Publication, 48, 69-90, 1998.
- [20] C.E. Oyarzún, R. Godoy, and S. Leiva, "Atmospheric deposition of nitrogen in a transect from the Central Valley to Cordillera de Los Andes, south-central Chile" *Revista Chilena de Historia Natural*, 75, 233-243, 2002.
- [21] S.S. Perakis, and L.O. Hedin, "Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds" *Nature*, 415, 416-419, 2002.
- [22] C.E. Oyarzún, R. Godoy, A. de Schrijver, J. Staelens, and N. Lust, "Water chemistry and nutrient budgets in an undisturbed evergreen rainforest of southern Chile" *Biogeochemistry*, 71, 107-123, 2004.
- [23] S. Carpenter, T. Frost, L. Persson, M. Power, and D. Soto, "Freshwater Ecosystems: Linkages of Complexity and Processes", 299-325, in H.A. Mooney, J.H. Cushman, E. Medina, O.E. Sala, and E.D. Schulze (eds.) *Functional Roles of Biodiversity: A Global Perspective*, J. Wiley & Sons Ltd., 1996.
- [24] M.A. Pascual, V. Cussac, B. Dyer, D. Soto, P. Vigliano, S. Ortubay, and P. Macchi, "Freshwater fishes of Patagonia in the 21st Century after a hundred years of human settlement, species introductions, and environmental change" *Aquatic Ecosystems Health & Management*, 10, 212-227, 2007.
- [25] O.E. Scaparti, L. Spescha, M.J. Fioriti, and A.D. Capriolo, "El Niño driven climate variability and drainage anomalies in Patagonian region, Argentina", *Cuadernos de Investigación Geográfica*, Universidad de La Rioja, 27, 179-191, 2001.
- [26] M. Latif, "El Niño/Southern Oscillation-Phenomenon: Dynamics and climatological impacts", 45-51, in J.L. Lozán, H. Graßl, and P. Hupfer (eds.) *Climate of the 21st century: Changes and risks*, 2nd ed., Wissenschaftliche Auswertungen, Hamburg, 2001.

- [27] V.R. Barros, V.H. Cordon, C.L. Moyano, R.J. Mendez, J.C. Forquera, and O. Pizzio, "Cartas de precipitación de la zona oeste de las provincias de Río Negro y Neuquén", Facultad de Ciencias Agrarias, Universidad Nacional del Comahue, Cinco Saltos, 40 pp, 1983.
- [28] N.D. Gordon, T. McMahon, B. Finlayson, C. Gippel, and R. Nathan, "Stream Hydrology. An Introduction for ecologists", Wiley, London, 2004.
- [29] E. Bianchi, "Estudio ecológico de la Pampa del Huenuleo (S. C. de Bariloche, Pcia. de Río Negro), Parte I: Geomorfología", Cuadernos Universitarios, Universidad Nacional del Comahue, 18 pp, 1987.
- [30] R.J. Albariño, "Spatial distribution of Plecoptera from an Andean-Patagonic lotic environment in Argentina" *Revista Brasileira de Biologia*, 57 (4), 629-636, 1997.
- [31] F.L. Pedrozo, S. Chillrud, P. Temporetti, and M.M. Díaz, "Chemical composition and nutrient limitation in rivers and lakes of northern Patagonian Andes (39.5°- 42°S; 71°W) (Rep. Argentina)", *Verhandlungen der Internationale Vereinigung für Limnologie*, 25, 207-214, 1993.
- [32] P.L. García, and D.A. Añón Suárez, "Community structure and phenology of chironomids (Insecta: Chironomidae) in a Patagonian Andean stream" *Limnologica*, 37, 109-117, 2007.
- [33] K.W. Cummins, and R.W. Merritt, "Ecology and distribution of aquatic insects", 74-86, in R.W. Merritt, and K.W. Cummins (eds.) *An introduction to the aquatic insects of North America*, Kendall/Hunt Publishing Company, Dubuque, 1996.
- [34] R. Albariño, and A. Valverde, "Hábito alimentario del estado larval de *Parasericostoma cristatum* (Trichoptera: Sericostomatidae)", *Revista de la Sociedad Entomológica Argentina*, 57, 131-135, 1998.
- [35] R.J. Albariño, "Dinámica del procesamiento de la materia orgánica particulada gruesa por el macrozoobentos en arroyos andinos", Doctoral Thesis, Universidad Nacional del Comahue, Bariloche, Argentina, 174 pp, 1999.
- [36] R.J. Albariño, "Food habit and mouthpart morphology of a South Andes population of *Klapopteryx kuscheli* (Plecoptera: Austroperlidae)" *Aquatic Insects*, 23, 171-181, 2001.
- [37] S.M. Velásquez, and M.L. Miserendino, "Habitat type and macroinvertebrate assemblages in low order Patagonian streams" *Archiv für Hydrobiologie*, 158, 461-83, 2003.
- [38] V. Díaz Villanueva, R. Albariño, and B. Modenutti, "Grazing impact of two aquatic invertebrates on periphyton from an Andean-Patagonian stream" *Archiv für Hydrobiologie*, 159, 455-471, 2004.
- [39] R.J. Albariño, and V. Díaz Villanueva, "Feeding ecology of two plecopterans in low order Andean-Patagonian streams" *International Review of Hydrobiology*, 91, 122-135, 2006.
- [40] J.M. Tierno de Figueroa, A. Vera, and M.J. Rodríguez, "Adult and nymphal feeding in the stonefly species *Antarctoperla michaelsoni* and *Limnoperla jaffueli* from central Chile (Plecoptera: Gripopterygidae)", *Entomologia Generalis* 29(1), 39-45, 2006.

- [41] R.M. Thompson, and C.R. Townsend, "The effect of seasonal variation on the community structure and food web attributes of two streams: implications for food-web science" *Oikos*, 87, 75-88, 1999.
- [42] R.J. Albariño, and E.G. Balseiro, "Leaf litter breakdown in Patagonian streams: native versus exotic trees and the effect of invertebrate size", *Aquatic Conservation: Marine and Freshwater Ecosystems*, 12, 181-192, 2002.
- [43] A.D. Rosemond, C.M. Pringle, and A. Ramirez, "Macroconsumers effects on insect detritivores and detritus processing in a tropical stream", *Freshwater Biology*, 39, 515-524, 1998.
- [44] T.V. Royer, and W. Minshall, "Controls on leaf processing in streams from spatial-scaling and hierarchical perspectives", *Journal of the North American Benthological Society*, 22(3), 352-358, 2003.
- [45] J.B. Wallace, J.R. Webster, S.L. Eggert, J.L. Meyer, and E.R. Siler, "Large woody debris in a headwater stream: long-term legacies of forest disturbance", *International Review of Hydrobiology*, 86, 501-513, 2001.
- [46] N.H. Anderson, and J.R. Sedell, "Detritus processing by macroinvertebrates in stream ecosystems", *Annual Review of Entomology*, 24, 351-377, 1979.
- [47] M.A.S. Graça, "The role of invertebrates on leaf litter decomposition in streams - a review", *International Review of Hydrobiology*, 86, 383-393, 2001.
- [48] C.V. Baxter, K.D. Fausch, and W.C. Saunders, "Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones", *Freshwater Biology*, 50, 201-220, 2005.
- [49] M.S. Wipfli, and D.P. Gregovich, "Invertebrates and detritus export from fishless headwater streams in southeast Alaska: Implications for downstream salmonid production", *Freshwater Biology*, 47, 957-970, 2002.
- [50] C.D. Snaddon, B.A. Stewart, and B.R. Davies, "The effect of discharge on leaf retention in two headwater streams", *Archiv für Hydrobiologie*, 125(1), 109-120, 1992.
- [51] T.T. Veblen, T. Kitzberger, B.R. Burns, and A.J. Rebertus, "Perturbaciones y regeneración en bosques andinos del sur de Chile y Argentina", 169-198, in: J.J. Armesto, M.K. Arroyo, C. Villagrán (eds.) *Ecología del Bosque Nativo de Chile*, Universidad de Chile Press, Santiago de Chile, 1996.
- [52] L.A. Smock, G.M. Metzler, and J.E. Gladden, "Role of debris dams in the structure and functioning of low-gradient headwater streams", *Ecology*, 70(3), 764-775, 1989.
- [53] A. Andreoli, G. Carlig, F. Comiti, and A. Iroumé, "Study on large woody debris in a stream from the Andes Mountains: functionality and importance", *Bosque*, 28(2), 83-96, 2007.
- [54] P. Diehl, M.J. Mazzarino, F. Funes, S. Fontenla, M. Gobbi, and J. Ferrari, "Nutrient conservation strategies in native Andean-Patagonian forests", *Journal of Vegetation Science*, 14, 63-70, 2003.
- [55] J.R. Webster, and E.F. Benfield, "Vascular plant breakdown in freshwater ecosystems", *Annual Review of Ecology and Systematics*, 17, 567-594, 1986.
- [56] S.F. Davis, and M.J. Winterbourn, "Breakdown and colonization of *Nothofagus* leaves in a New Zealand stream", *Oikos*, 28, 250-255, 1977.

- [57] J.S. Rounick, and M.J. Winterbourn, "Leaf processing in two contrasting beech forest streams: effects of physical and biotic factors on litter breakdown", *Archiv für Hydrobiologie* 96, 448-474, 1983.
- [58] W. Linklater, "Breakdown and detritivore colonisation of leaves in three New Zealand streams", *Hydrobiologia*, 306, 241-250, 1995.
- [59] M.A. Chadwick, and A.D. Huryn, "Effect of a whole-catchment N addition on stream detritus processing", *Journal of the North American Benthological Society*, 22, 194-206, 2003.
- [60] W.F. Cross, J.P. Benstead, A.D. Rosemond, and J.B. Wallace, "Consumer-resource stoichiometry in detritus-based streams", *Ecology Letters*, 6, 721-732, 2003.
- [61] R.J. Albariño, and E.G. Balseiro, "Food quality, larval consumption, and growth of *Klapopteryx kuscheli* (Plecoptera: Austroperlidae) from a south Andes stream", *Journal of Freshwater Ecology*, 16, 517-526, 2001.
- [62] R. Albariño, V. Díaz Villanueva, and C. Canhoto, "The effect of sunlight on leaf litter quality reduces growth of the shredder *Klapopteryx kuscheli*", *Freshwater Biology*, 53, 1881-1889, 2008.
- [63] M.O. Gessner, and J.S. Schwoerbel "Fungal biomass associated with decaying leaf litter in a stream", *Oecologia*, 87, 602-603, 1991.
- [64] M.O. Gessner, and E. Chauvet, "Importance of stream microfungi in controlling breakdown rates of leaf litter", *Ecology*, 75, 1807-1817, 1994.
- [65] J.S. Richardson, "Seasonal food limitation of detritivores in a montane stream: an experimental test", *Ecology*, 72, 873- 887, 1991.
- [66] E.F. Benfield, J.R. Webster, J.L. Tank, and J.J. Hutchens, "Long-term patterns in leaf breakdown in streams in response to watershed logging", *International Review of Hydrobiology*, 86, 467-474, 2001.
- [67] S.L. Eggert, and J.B. Wallace, "Litter breakdown and invertebrate detritivores in a resource-depleted Appalachian stream", *Archiv für Hydrobiologie*, 156(3), 315-338, 2003.
- [68] M.C. Molles, "Trichopteran communities of streamms associated with aspen and conifer forests: long-term structural change" *Ecology*, 63(1), 1-6, 1982.
- [69] M.A.S. Graça, J. Pozo, C. Canhoto, and A. Elósegí, "Effects of *Eucalyptus globulus* plantations on detritus, decomposers, and detritivores in streams" *The Scientific World Journal*, 2, 1173-1185, 2006.
- [70] C. Valdovinos, "Procesamiento de detritus ripariano por macroinvertebrados bentónicos en un estero boscoso de Chile central" *Revista Chilena de Historia Natural*, 74, 445-453, 2001.
- [71] N. Friberg, and D. Jacobsen, "Feeding plasticity of two detritivore – shredders" *Freshwater Biology*, 32, 133-142, 1994.
- [72] J.V. Ward, "Aquatic Insect Ecology. 1. Biology and Habitat", J. Wiley & Sons, New York, 438 pp, 1992.
- [73] R.W. Merritt, and K.W. Cummins, "An Introduction to the Aquatic Insects of North America", Kendall/Hunt Publishing Company, Dubuque, 1996.

- [74] K.J. Collier, and M.J. Winterbourn, "New Zealand stream invertebrates: ecology and implications for management", The Caxton Press, Christchurch, 415 pp, 2000.
- [75] A. Valverde, and R. Albariño, "Descripción de los estados inmaduros de *Myotrichia murina* y *Parasericostoma cristatum* (Trichoptera: Sericostomatidae)" Revista de la Sociedad Entomológica Argentina, 58, 11-16, 1999.
- [76] C. Nieto, "South American Baetidae (Ephemeroptera): a New Generic Synonymy" Studies on Neotropical Fauna and Environment, 39(2), 95-101, 2004.
- [77] A. Vera, and A. Camousseight, "Estado de conocimiento de los plecópteros de Chile" Gayana, 70(1), 57-64, 2006.
- [78] A. Palma, and R. Figueroa, "Latitudinal diversity of Plecoptera (Insecta) on local and global scales" Illiesia, 4(8), 81-90, 2008.
- [79] M. Dobson, and A.G. Hildrew, "A test of resource limitation among shredding detritivores in low order streams in southern England" Journal of Animal Ecology, 61, 69-77, 1992.
- [80] M. Abelho, and M.A.S Graça, "Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in Central Portugal" Hydrobiologia, 324, 195-204, 1996.
- [81] K.M. Wantzen, and R. Wagner, "Detritus processing by invertebrate shredders: a neotropical-temperate comparison" Journal of the North American Benthological Society, 25(1), 216-232, 2006.
- [82] G.W. Minshall, R.C. Petersen, K.W. Cummins, T.L. Bott, J.R. Sedell, C.E. Cushing, and R.L. Vannote, "Interbiome comparison of stream ecosystem dynamics" Ecological Monographs, 53, 1-25, 1983.
- [83] H. Campos, J. Arenas, C. Jara, T. Gonser, and R. Prins, "Macrozoobentos y fauna íctica de las aguas limnéticas de Chiloé y Aysén continentales (Chile)" Medio Ambiente, 7, 52-64, 1984.
- [84] I.R. Wais, and A.A. Bonetto, "Analysis of the allochthonous organic matter and associated macroinvertebrates in some streams of Patagonia (Argentina)" Verhandlungen der Internationale Vereinigung für Limnologie, 23, 1455-1459, 1988.
- [85] L.I. de Cabo, and I.R. Wais, "Macrozoobenthos prospection in central Neuquen streams, Patagonia, Argentina" Verhandlungen der Internationale Vereinigung für Limnologie, 24, 2091-2094, 1991.
- [86] R.D. Moore, and J.S. Richardson, "Progress towards understanding the structure, function, and ecological significance of small stream channels and their riparian zones" Canadian Journal of Forest Research, 33, 1349-1351, 2003.
- [87] L. Buria, R.J. Albariño, V. Díaz Villanueva, B. Modenutti, and E. Balseiro, "Impact of exotic rainbow trout on the benthic macroinvertebrate community from Andean-Patagonian headwater streams" Archiv für Hydrobiologie, 168 (1), 145-154, 2007.
- [88] L.M. Buria, "Efecto de la depredación en la estructuración comunitaria del zoobentos en ambientes lóticos norpatagónicos", Doctoral Thesis, Universidad Nacional del Comahue, Bariloche, Argentina, 145 pp, 2008.

- [89] C.R. Townsend, "Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams" *Conservation Biology*, 17, 38-47, 2003.
- [90] H.S. Greig, and A.R. McIntosh, "Indirect effects of predatory trout on organic matter processing in detritus-based stream food webs" *Oikos*, 112, 31-40, 2006.
- [91] L.M. Buria, R.J. Albariño, B.E. Modenutti, and E.G. Balseiro, "Temporal variations in the diet of the exotic rainbow trout (*Oncorhynchus mykiss*) in an Andean-Patagonian canopied stream", *Revista Chilena de Historia Natural*, in press.