Diversity and growth of epiphytic macrolichens in northwestern Patagonian *Nothofagus* forests

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Abstract

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This thesis focuses on distribution and ecology of epiphytic lichens in *Nothofagus* forests of northwestern Patagonia, Argentina. The general aims were 1) to analyse diversity and abundance of epiphytic lichen vegetation in gradients of stand age and humidity and 2) to study growth rates and decomposition of important macrolichen species.

Gradients in biomass and species diversity of epiphytic macrolichen communities are positively correlated to increasing annual precipitation. This pattern was particularly clear for the cyanolichen species of the genus *Pseudocyphellaria*. Lichen biomass and diversity increases with stand age but colonization of young stands is probably also influenced by the presence of remnant old trees and the distance to old-growth forest. In old-growth-forests, the nitrogen input by N-fixing cyanolichens can be significant, mostly due to the abundance of tripartite *Pseudocyphellaria* and *Nephroma* species. Surveys of trunks and litter provide supplementary information. However, future studies should also include surveys of canopy branches in order to give representative information on lichen abundance and diversity.

Growth and decomposition showed a similar seasonal pattern with highest rates recorded during winter for all macrolichens analysed. Constantly humid conditions may favour both processes during the winter season. Annual growth rates of *Pseudocyphellaria berberina* showed a 10-20% increase in biomass. No differences in growth rates depending on transplanting method, phorophyte age or stand age could be found. It is concluded that limitations in dispersal or establishment are more important than stand microclimate for performance of *P. berberina* in post-fire stands. Cyanolichens with highest nitrogen content showed the lowest decomposition rates, contrary to what was expected. This supports the hypothesis of the presence of an anti-herbivore component in the *Lobariaceae* family in southern temperate forests. Post-fire sequences are well suited to study effects of disturbance on lichen distributions in *Nothofagus* forests. Further studies are needed to analyze the effect of gap size and remnant trees on recolonization of epiphytic lichens. Such information will be essential to predict effects of forestry in previously unmanaged forest landscapes.

Keywords: lichen distribution, epiphytic macrolichens, growth rate, decomposition, lichen diversity, lichen abundance, *Nephroma*, *Pseudocyphellaria*, *Sticta, Nothofagus* forest.

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Appendix

Papers I-IV

This thesis is based on the following papers, which are referred to in the text by the corresponding Roman numerals, I-IV.

I. Caldiz, M.S. & Brunet, J. Distribution patterns of foliose macrolichens in northern Patagonian *Nothofagus* forests – a comparison of trunk surveys and litter sampling. (*Manuscript).*

II. Caldiz, M.S. & Brunet, J. Epiphytic lichen litter abundance in *Nothofagus* forests of northern Patagonia, Argentina: relation to stand age and humidity. Austral Ecology *(under revision).*

III. Caldiz, M.S. 2004. Seasonal growth pattern in the lichen *Pseudocyphellaria berberina* in north-western Patagonia. Lichenologist 36: 435-444.

IV. Caldiz, M.S., Brunet, J. & Nihlgård, B. Lichen litter decomposition in *Nothofagus* forest of northern Patagonia: biomass and chemical changes over time. The Bryologist *(under revision).*

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Introduction

Preservation of biological diversity is a major concern for modern societies. A major difficulty in preserving biological diversity is that so much is still unknown (Magurran, 2004), and this is certainly true of lichens (Ahmadjian, 1995). Much of the global biodiversity is found in forests, and so most of the threatened species pool is found there (Hanski & Hammond, 1995). Today, forest fragmentation and habitat destruction are threatening many species around the world. Many lichen species are confined to forests, including many species that are still unknown or sketchily described with very little information about their distribution, life traits or ecology.

Studies of the ecology and preservation of forest ecosystems in Patagonia have a very short history. So far, studies have mostly focused on tree and vascular plant ecology and their taxonomy (Galloway, 1995; Veblen *et al.*, 1996; Armesto, Villagran & Kalin Arroyo, 1997; Donoso *et al.*, 2004). Local ecological studies of groups such as cryptogams, fungi and insects only started a few years ago, and only a few studies have focused on the taxonomy and chemistry of cryptograms.

This thesis focuses on the distribution and ecology of epiphytic lichens in *Nothofagus* forests in northwestern Patagonia. Papers **I**-**II** consider macrolichen diversity and abundance in relation to distribution, age and structure of *N. dombeyi* and *N. pumilio* forests. Paper **III** explores growth rates of one common lichen species, *Pseudocyphellaria berberina*, and the possibility of using the results as a basis for conservation and further physiological experiments. Paper **IV** deals with the decomposition rates and nutrient release of five of the most abundant lichens considered in paper **II**.

Lichens

Lichens are defined as symbiotic organisms composed of a mycobiont (fungal partner) and photobiont (photosynthetic partner). The photobiont may be either a green alga or a cyanobacterium (Hawksworth & Honegger, 1994). The two kinds of photobionts may even be represented in the same thallus, implying that three kingdoms are represented in one “individual” (Nash III, 1996a). Lichens comprising green photobionts and cyanobionts are called tripartite lichens. The majority of lichens have green algae as a photobiont, and the rest have a cyanobacterium as the primary photobiont. Only a small number of those cyanolichens have both a cyanobacterium and algae. In the tripartite lichens, the function of the cyanobiont is mostly to produce nitrogen for the whole thallus.

The lichen group is polyphyletic and appeared on earth at different times during evolution. The first lichens probably developed around 440 million years ago, and preceded even the first plants (Willis & McElwain, 2002). Since then, they have colonised almost all habitats and extreme conditions, from epiphytic (growing on trees) to endolithic (growing under the surface of rocks), and from Antarctica to the highest mountains and sea shores (Nash III, 1996a).

Lichen diversity

Lichen species are usually defined by the mycobiont, which determines the morphology and chemical composition of the thallus (Ahmadjian, 1993) but the importance of the photobiont for the systematics of lichens has also been debated (Rambold, Friedl & Beck, 1998). The number of lichen species in the world is estimated to be around 13,500 (Galloway, 1992a).

Temperate forests are ecosystems with complex dynamics that contain a great variety of habitats for different species. Most temperate forests are under disturbance regimes such as gap dynamics or large-scale disturbances. Successional changes in the host forest produce differences in lichen habitats, such as changes in light penetration, and host tree bark characteristics (McCune & Antos, 1982). More complex structured forests usually harbour higher diversity. Old forests are structurally more complex and so contain greater epiphytic lichen biomass than young forests, and many epiphytic species are closely associated with old-growth (Lesica *et al.*, 1991; Esseen, Renhorn & Petersson, 1996; Dettki & Esseen, 1998; Sillett & Goward, 1998). Forest continuity has been shown to play a major role in the presence and abundance of lichen species (Rose, 1976). Lichen communities respond to temporal changes through a number of processes, ranging from traditional Clementsian succession to competitive displacement hierarchies (Yarranton, 1972). This can be seen as a gradual replacement of pioneer state by climax associations (Kantvilas & Jarman, 2004). Changes in lichen communities over time do not necessarily reflect succession, and it has been postulated that they might instead reflect changes in patterns of species diversity due to dispersal ability (McCune & Antos, 1981; Begon, Harper & Townsend, 1996).

Functional role of lichens in ecosystems

Epiphytic lichens are important components in many forest ecosystems. As well as contributing to species diversity, lichens also provide nesting material, food, and refugia for other organisms (Esseen, Renhorn & Petersson, 1996). Lichens in the form of litterfall are an important source of nitrogen in nitrogen-limited forest ecosystems (Sollins *et al.*, 1980), as well as being a source of micronutrients such as iron (Knops *et al.*, 1991). Lichen tissue contains nitrogen largely in the form of proteins and chitin with smaller amounts of soluble amino acids and nucleic acids (Greenfield, 1993). Several lichens contain N-fixing cyanobacteria, providing a net input to the forest ecosystem during decomposition (Green *et al.*, 1980). Various studies around the world show that values of nitrogen input vary from 2 to 17 kg N ha^{-1} yr^{-1} (Green *et al.*, 1980; Antoine, 2004).

Lichen species differ considerably in their rates of weight loss and decomposition (Moore, 1984; McCune & Daly, 1994). Microclimate seems to have a profound influence on the rate of lichen decomposition (Wetmore, 1982; Moore, 1984; Greenfield, 1993).

Growth

Lichens are generally considered as slow-growing organisms, and several reasons have been suggested for this. Firstly, they are poikilohydric, *i.e.* they depend of water from the atmosphere and cannot regulate their water content; secondly, the fungal content in the thallus is high; and thirdly, nitrogen has been shown to be a limiting factor for growth in lichens in which cyanobacteria are not the photobiont (Sundberg *et al.*, 1997; Sundberg, Näsholm & Palmqvist, 2001). The poikilohydric nature of lichens restricts photosynthesis to periods with high air humidity (Palmqvist & Sundberg, 2000). In temperate climates, lichen growth is usually strongly seasonal, although species studied so far show great dissimilarity in the season when growth occurs (Armstrong, 1973; Armstrong, 1993; Muir, Shirazi & Patrie, 1997). The majority of studies conclude that growth is correlated to precipitation, thereby explaining most of these variations (Hale, 1970; Armstrong, 1973; Armstrong, 1993; Muir, Shirazi & Patrie, 1997). In recent years, studies of the growth of different lichen forms have become more common, usually with a focus on ecological and conservational issues as well as their use in monitoring pollution (Armstrong, 1973; Armstrong, 1993; McCune *et al.*, 1996; Muir, Shirazi & Patrie, 1997; Renhorn *et al.*, 1997; Calvelo *et al.*, 2002; Hedenås, 2002).

Dispersal and establishment

One of the most discussed factors affecting the occurrence and distribution of lichens in forest is their reproductive and dispersal mechanisms. Lichens disperse by two main strategies: sexual and asexual (or vegetative). In sexual dispersal, the fungus reproduces and disperses alone and depends on the presence of an algae or a cyanobacterium to form a new thallus. In asexual dispersal, propagules contain both photobiont and mycobiont; these propagules can be soredia, isidia or thallus fragments (Nash III, 1996a). Though lichens usually have one main dispersal strategy, some species can have both. Lichens are usually passively dispersed and the dispersal agent can be wind, water or animals (Bailey, 1976).

For some lichen species it has been proved that dispersal is the main limiting factor (Sillett *et al.*, 2000). Furthermore, experiments have shown that vegetative diaspores of some species establish indistinctly in young or old-growth forest (Sillett *et al.*, 2000; Hilmo & Såstad, 2001). However, few studies have looked at the microsite conditions in which lichens can survive and reproduce (Gauslaa, Ohlson & Rolstad, 1998; Hilmo, 2002; Hilmo & Holien, 2002).

Nothofagus forests and their lichen flora in northwestern Patagonia

The austral forests of South America stretch in a narrow band from 35° S to Tierra del Fuego at 56° S (Fig. 1). Most of these forests are classified as temperate. One of the outstanding characteristics of the austral forests is their high degree of endemism. One-third of the vascular flora is estimated to be endemic. A high degree endemism is also found in the fauna and non-vascular flora. This is usually explained by the long and pronounced isolation the region has experienced (Armesto, Leon-Lobos & Kalin Arroyo, 1997). Forests are continuous from the timberline in the high mountains to the coast on the occidental side of the Andes, except for the man-modified central valley. On the eastern side of the Andes, the forest belt is thin, dominated by *Nothofagus* and *Austrocedrus chilensis,* which soon gives away to steppe ecosystems when annual precipitation drops below 500 mm.

Forest types

The vegetation pattern in Patagonia is strongly related to precipitation and temperature. Precipitation decreases from W to E. The western slopes of the Andes receive orographic rain with annual precipitation exceeding 5,000 mm, while on the eastern part of the mountains, annual rainfall drops rapidly from 3,000 to 800 mm in less than 50 km (Veblen *et al.*, 1996).

There are seven species of *Nothofagus* in South America, and their distribution is controlled by the climatic gradients mentioned earlier. Temperature decreases with altitude and latitude, producing a gradient from an evergreen forest to deciduous *N. pumilio* and *N. antarctica* forests in the high mountains and the very south. In Northern Patagonia two main forest types, the Valdivian rainforest and the cool temperate Patagonian forest, prevail between 37° 45’ S and 43° 20’ S (Veblen, Schlegel & Oltremari, 1983). Although the Valdivian rainforest occurs mainly on the Chilean side of the Andes, some extensions on the Argentinian side of the Andes are found in lower areas where humid air masses can pass through the mountain range (Veblen *et al.*, 1996; Fig. 1).

Valdivian forests are dominated by evergreens, with a few deciduous and coniferous species. At low elevations, ten to 15 tree species (mostly termophyllous evergreen species) are found together, including the dominant evergreen, *N. dombeyi*, and the deciduous *N. obliqua* and *N. alpina*. In contrast, Patagonian or Magellanic forest types situated in the west of the Andes or in the south have only two to three species. The understorey is dominated by bamboo (*Chusquea sp*.). On low precipitation sites, the evergreen *Nothofagus dombeyi* dominates while at higher altitudes or in xeric locations, *N. pumilio* and *N. antarctica* dominate. Coniferous forests are represented in the west by *Fitzroya cupressoides* and other species such as *Podocarpus nubigena* and *Saxegothea conspicua*. Low precipitation sites have mixed stands of *N. pumilio* and *Austrocedrus chilensis* or pure *A. chilensis* stands.

Nothofagus has been the dominant tree genus for the last 14,000 years at the 40th latitudes on both sides of the Andes. Around 10,000 years ago, the climate became gradually warmer and moister and allowed more tree genera to colonize the area. Since 3,000 years ago, the forest composition has remained rather stable (Markgraf, Romero & Villagran, 1996).

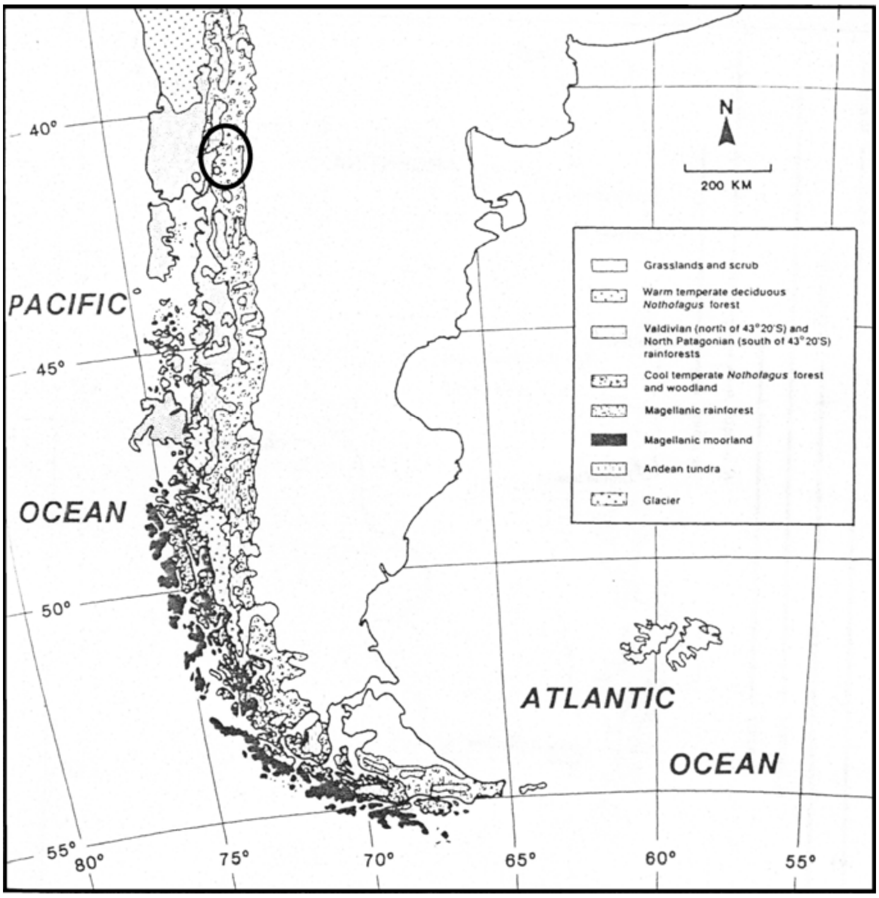

Fig. 1. Major vegetation zones of southern South America. The circle shows the study area. After Veblen *et al.* (1996).

Forest dynamics

The dynamics of the southern South American *Nothofagus* forests are mainly driven by a coarse-scale disturbance regime dominated by landslides, glacier retreat or fires produced by volcanic activity, lightning ignition or anthropogenic sources. These types of events usually allow the establishment of shade-intolerant species. Around 40° S latitude, in the study area of this project, fire is the dominating disturbing agent for stand replacement and tree regeneration. Disturbances create regeneration opportunities for shade-intolerant species such as *Nothofagus* species, *Austrocedrus chilensis* and *Araucaria araucana*. The *Nothofagus* spp. forests form even-aged cohorts following coarse-scale disturbances. In the absence of large disturbances, fine-scale treefall gaps drive the regeneration of these species.

The tree species studied in this work were *N. dombeyi* and *N. pumilio. Nothofagus dombeyi* is a shade-intolerant evergreen species that, in coexistence with shade-tolerant Valdivian species, depends on landslides or fire for regeneration. In the study area, it occurs up to altitudes of 1,500 m, and to the east it forms mixed stands with *Austrocedrus chilensis* until annual precipitation reaches around 1,000 mm. *Nothofagus dombeyi* trees can reach up to 50 m in height with diameters of up to two metres. Deciduous *N. pumilio* forest dominates at higher altitudes from 1,200 m up to the timberline (approximately 1,700 m). Regeneration of *N. pumilio* is associated with both coarse and fine scale disturbances. In some areas regeneration is severely restricted by bamboo at a fine scale level. The morphology of *N. pumilio* changes from erect tree stands at lower altitudes to krummholz in the higher altitudes near the timberline.

Management and conservation

Nothofagus forests on both sides of the Andes have been subjected to exploitation, and have been replaced in large areas by exotic coniferous plantations. This is most evident on the Chilean side although large areas were also planted on the Argentinian side. In Argentinian Patagonia, *N. dombeyi* and *N. alpina* forests are managed today for silviculture.

There are impressive areas of nature reserves and national parks on both sides of the Andes (Ortiz et al., 1993). Between the 37° S and 42° S latitudes, the protected areas total up to 1,750,000 ha (http://www.conaf.cl; 1-March-2005; http://www.parquesnacionales.gov.ar; 1-March-2005). However, the protection of *Nothofagus* forests might not be adequate since we lack information about whether the variety of *Nothofagus* environments is adequately represented in the existing reserves.

Lichen flora of *Nothofagus* forests

South American temperate *Nothofagus* forests are characterised by high lichen diversity and high biomass of foliose species (Santesson, 1940; Galloway, 1995). The high humidity and extreme topography make these forests some of the most diverse in the world in terms of biomass and epiphytic lichens. One of the most abundant epiphytic lichen groups in Patagonian temperate forests are the *Lobariaceae*, with a high abundance and diversity of *Pseudocyphellaria* and *Sticta*. Many of the *Pseudocyphellaria* species can reach a large size and build up a considerable biomass at stand scale. Though some of the species are widespread, *Pseudocyphellaria* has an important endemic element within South America, 72% of the species are found only on the southern part of the continent (Galloway, 1992b).

Twenty-nine of the South American *Pseudoyphellaria* species (55%) contain cyanobacteria as primary photobionts. The rest have green algae but also contain cyanobacteria in cephalodia, representing an important part of atmospheric nitrogen fixation in the ecosystem (Green *et al.*, 1980; Galloway, 1988; Guzman, Quilhot & Galloway, 1990). For New Zealand temperate rainforest the nitrogen contribution was suggested to be between 1 and 10 kg N ha^{-1} y^{-1} for the large foliose species (*Pseudocyphellaria* and *Sticta*) (Green *et al.*, 1980). In South America the proportion of species with cyanobacterial symbionts is higher, suggesting a greater input of nitrogen for this rainforest (Guzman, Quilhot & Galloway, 1990; Galloway, 1992b).

Lichen conservation

Conservation of lichens has a short history, starting in Europe in the 1960s and 1970s with reports on changes in lichen communities due to air pollution. Though some research started in the 1970s, it was not until the 1990s that impact of forestry and the importance of old-growth and forest continuity became more widely acknowledged in Europe and USA (Rose, 1976; Lesica *et al.*, 1991; Rose, 1992).

In European forests, human activities have been shown to have severe and long-lasting effects on epiphytic lichens, especially in temperate forests. Air pollution and forest management in particular have greatly reduced the abundance and distribution of many lichen species (Rose, 1992). Logging has altered the pre-settlement stand age mosaic by systematically converting old-growth to second growth. As a result, some species have become more common, while many others have decreased. Although many species can occur in stands of all ages, others are more restricted to certain ages (Lesica *et al.*, 1991). In addition, landscape fragmentation may physically reduce the size of the habitat and increase the distance between the remaining fragments (Fahrig, 1997). Consequently, forest continuity is an important factor affecting lichen diversity, distribution and abundance (Rose, 1976; Hyvärinen, Halonen & Kauppi, 1992; McCune, 1993). In small and isolated populations, reduced genetic variation can be expected because genetic drift becomes an increasingly important process as population size decreases (Soulé, 1987).

Rare and endangered species can be preserved in different ways – by establishing nature reserves, implementing proper forest management regimes that are compatible with long-term viability of lichen communities or by artificial dispersal of endangered species (Neitlich & McCune, 1997; Peck & McCune, 1997; Liden *et al.*, 2004). Information about ecological mechanisms that drive the population dynamics of epiphytic lichens might help to create policies of forest management or help to locate suitable areas in which these communities can survive.

Very few ecological lichen studies have been conducted in southern temperate *Nothofagus* forests, especially in Patagonia and the eastern Andean slopes (Galloway, 1995). A serious problem for such studies is the lack of a complete lichen flora (Galloway, 1992a, 1995). However, except for natural and anthropogenic fires, large areas of forest in Patagonia have virtually no history of human impact or management. Therefore, information about the distribution and abundance of epiphytic lichens gives a unique opportunity to test assumptions about the natural distribution and patterns of lichen biomass and diversity in similar ecosystems in other parts of the world with histories of anthropogenic changes.

Objectives

The general aims of this thesis are to analyse diversity and abundance of epiphytic lichen vegetation in gradients of stand age and humidity and to study growth rates and decomposition of some of the most abundant macrolichen species in *Nothofagus* forests in northwestern Patagonia.

Specific aims are:

I. to compare distribution patterns of the three most abundant lichen genera in relation to humidity and stand age.

II. to compare lichen litterfall biomass and taxon richness in a) young and old-growth and b) low and high precipitation *Nothofagus* forests.

III. to analyse seasonal growth dynamics of the macrolichen *Pseudocyphellaria berberina*.

IV. to analyse seasonal patterns of litter decomposition and nutrient release of the common macrolichens *Pseudocyphellaria flavicans*, *P. faveolata*, *Nephroma antarcticum*, *Platismatia glauca* and *Protousnea magellanica*.

Methods

All studies in this thesis were conducted in the Nahuel Huapi National Park, Argentina (centred at 40^{o} 53' S, 71^{o} 28' W). The area is located on the eastern slopes of the Andes, in northwestern Patagonia. Due to orographic rain, there is a great variation in precipitation in the studied area, ranging from 3,000 to 800 mm per year decreasing from west to east over a distance of only 50 km (Veblen *et al.*, 1996). The mean annual temperature is around 9 °C (Dimitri, 1972). Precipitation occurs mostly during autumn and winter with only 12% of the annual precipitation falling during summer.

Nahuel Huapi National Park is a vast area of protected land, comprising 705,000 ha. In 1903 Dr. Francisco P. Moreno donated part of today’s area to the state on condition that it remained untouched. It became the first South American national park in 1922 (http://www.parquesnacionales.gov.ar). Today, the area is divided into different degrees of protection. This thesis considered only pristine to very moderate anthropogenically disturbed areas.

Table 1. *Nothofagus dombeyi* and *N. pumilio* stands studied in papers I-IV.

Site	Name	Geographic position	Altitude (m. a.s.l.)	Mean annual precipitation (mm)	Age (yrs)	Paper
N. dombeyi						
Low precipitation						
LL Y	Llao llao young	41° 03’ S 71° 31’ W	760	1,700	90	I-II
LL O	Llao llao old	41° 14’ S 71° 16’ W	760	1,700	>200	I-II
LE Y	L. Correntoso young	40° 37’ S 71° 39’ W	850	2,000	60	I-II
LE O	L. Espejo Chico old	40° 35’ S 71° 43’ W	850	2,000	>150	I-II
High precipitation						
HF Y	N coast of L. Espejo, young	40° 31’ S 71° 45’ W	800	2,700	45	II
HF O	N coast of L. Espejo, old	40° 32’ S 71° 45’ W	800	2,700	>200*	II
HP Y	Puyehue Pass, young	41° 14’ S 71° 16’ W	760	2,800	60	II
HP O	Puyehue Pass, old	41° 14’ S 71° 16’ W	790	2,800	150	II
HB Y $_1$	Pto. Blest, young	41° 01’ S 71° 48’ W	760	3,000	60	III
HB Y $_2$	Pto. Blest, young	41° 01’ S 71° 48’ W	760	3,000	90	I-II
HB O	Pto. Blest, old	41° 01’ S 71° 49’ W	810	3,000	>150	I-II-IV
N. pumilio						
LCpu (*low precipitation*)	Co. Challhuaco	41° 14’ S 71° 16’ W	1,200	800	>150	I-II
HPpu (*high precipitation*)	Puyehue	40° 43’ S 71° 54’ W	1,300	2,800	>150	I-II

All the studies were carried out in the western part of the National Park, where the *Nothofagus* forests are located. The study areas in Papers **I-II** were situated in *N. dombeyi* and *N. pumilio* forests within the Nahuel Huapi National Park. The sites used in Papers **III-IV** were located in the area of Pto. Blest, in the very western part of Nahuel Huapi (41° 01’S, 71° 48’ W [WGS 84]). This area is an ingression of the Valdivian forest with annual precipitation of 3,000 mm, and a typical Valdivian vegetation component (Table 1).

Studied species

The studies focused on different lichen species. Epiphytic macrolichens were studied in Paper **I** with a focus on the family *Lobariaceae* and the genera *Pseudocyphellaria, Sticta* and *Nephroma*. In Paper **III** the focus was on *P. berberina* due to its great abundance and wide distribution. Paper **IV** looked at five of the most common macrolichen species found in the litterfall (**II**), i.e. *P. flavicans, P. faveolata, Nephroma antarcticum* and *Platismatia glauca* among the foliose lichens and *Protousnea magellanica* among the fruticose lichens.

Pseudocyphellaria berberina (G. Forster) D. Galloway & P. James is an epiphytic foliose lichen with thalli 10-20 cm in diameter, growing loosely attached to the substrate. The primary photobiont is green but has cyanobacteria in cephalodia, the medulla is yellow, the pseudocyphellae are on the lower surface and the lichen lacks asexual reproductive structures. *Pseudocyphellaria berberina* is endemic to the temperate Andean region in South America and the Southern Islands (Galloway & James, 1977). This lichen is most abundant in humid areas and grows on many different phorophytes. Its geographical distribution stretches from 39^{o} S to Tierra del Fuego, the southern Atlantic islands and Juan Fernandez Island (Galloway, 1992b; Fig. 2).

Pseudocyphellaria flavicans (J.D. Hook & Taylor) Vainio is a foliose species with a thallus of 5 – 15 cm diameter with free and ascending margins. The primary photobiont is green but has cyanobacteria in cephalodia, the medulla is yellow, and the pseudocyphellae are on the lower surface. It is corticolous and occasionally saxicolous. It has marginal and laminal isidia (Galloway, 1992b; Fig.2).

Pseudocyphellaria faveolata (Delise) Malme is a foliose species with narrow to broad lobes, and entire margins with prominent white pseudocyphellae. The primary photobiont is green but has cyanobacteria in cephalodia, and the medulla is white. The upper surface is faveolate with marginal, subpedicelate apothecia. It is distributed from latitude 37^{o} 60' S to Tierra del Fuego and Staten Island. It is also found in New Zealand and Tasmania (Galloway, 1992b).

Nephroma antarcticum (Jacq.) Nyl. var *antarcticum* is an epiphytic foliose lichen with thalli 10-15 cm in diameter. The primary photobiont is green but has cyanobacteria in cephalodia on the lower surface. It is pale grey-green to bright yellow. The apothecia are common on the lower surface. It is a widespread species in temperate South America. (White & James, 1988)

Platismatia glauca (L.) Culb. & Culb. is an epiphytic foliose lichen. The thallus is 3-10 cm in diameter, has numerous thin, irregular lobes, which stand up with ragged margins. The thallus is a pale greenish-grey to tan when dry, becoming green to olive or greenish-grey or tan when wet. The lower surface is smooth, shiny, irregularly mottled brown and white, and lacks rhizines. Lacking apothecia, the species has soredia and occasionally isidia. This species is common in the northern hemisphere, too.

Protousnea magellanica (Mont.) Krog comb. nov. is a fruticose lichen, with a corticolous, pendulous, flaccid, and a thallus up to 30 cm long. Primary branches are 1mm wide with dichotomous branching at first but then dissolving into a mass of capillaceous secondary branches. It has a fragile cortex at the base with several transversal cracks. Apothecia are 1-3.2 mm on thin and thick branches. It is one of the most common species of the genus and it is distributed from sea level up to 1,300 m in South American *Nothofagus* forests (Krog, 1976).

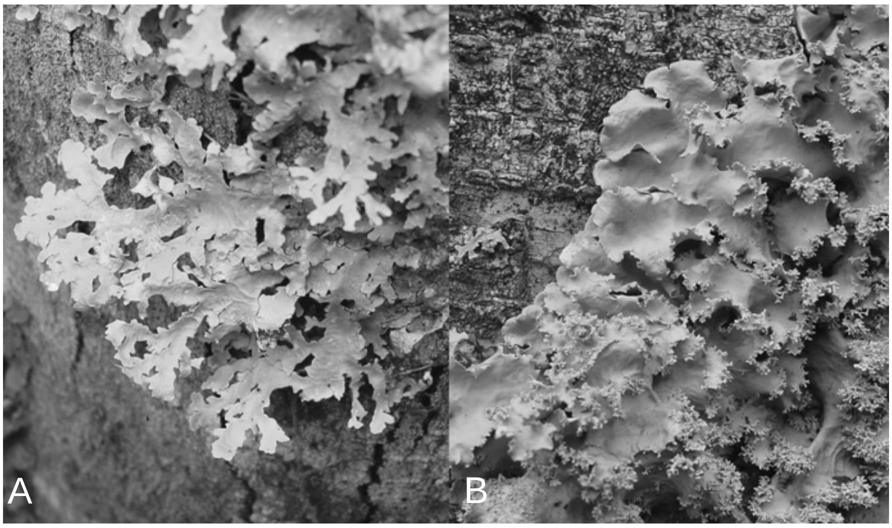

Fig 2. A: *Pseudocyphellaria berberina* and B: *P. flavicans* on *Nothofagus dombeyi* stems.

Papers I-II

In order to measure lichen diversity, a preliminary study was carried out in four stands in the high precipitation *N. dombeyi* forest in Pto. Blest. The age of the stands ages was 60, 90 and >200 years (two old-growth stands). In each stand epiphytic lichens were surveyed on 30, 45 and 15 trees respectively (see Paper **I** for surveying methodology). In cases when identification to species level in the field was not possible, lichens were grouped into morphogroups or to the lowest identifiable taxonomic level. This was mostly done for the crustose group and some genera of the foliose and fruticose species. The results of the pilot study are not included in Paper **I** but are partly presented in the results section below.

In order to compare the effect of stand age on the diversity and abundance of epiphytic lichens, five sites with *N. dombeyi* and two stands of *N. pumilio* forests were selected in both young (post-fire cohorts <100 years of age) and old stands (> 200 years). The occurrence of species within the genera *Nephroma* (*Nephromataceae*), *Pseudocyphellaria* and *Sticta* (*Lobariaceae*) was surveyed on the stems (up to 1.8 m above ground) of 15 randomly chosen trees within each stand. Abundance of each species was estimated according to the Braun-Blanquet scale (Westhoff & van der Maarel, 1973) in three height sections of 0.6 metres (a, b, c) on the northern and southern exposed parts of the trunk, resulting in six sample areas per trunk (**I**). In all stands, lichen fragments were collected from the forest floor in randomly located circular plots of 2 m radius (**II**).

Paper III

Seasonal growth of *P. berberina* was analysed by weighing thalli fragments (transplants) attached to trees or a hanging rack in the forest over a two-year period. The details of this method are described by McCune *et al.* (1996) and can be briefly described as follows. Outer lobes of *P. berberina* thalli were collected in the field, taken to the laboratory, air dried and weighed. They were then attached to hanging devices (a 3-cm nylon loop and a silicone sealant dab) and brought back to the forest. Every 3 months over a two-year period, the transplants were brought to the lab for weighing. The moisture content in the thallus was adjusted using the reference sample method for weight adjustment (McCune *et al.*, 1996). For this, 20 transplants were kept in the lab during the study period.

Fig. 3. *Nothofagus dombeyi* post-fire stand (90 years old) at Pto. Blest. It appears as a dense homogeneous canopy with some remnant trees outstanding. Note at the left, the limit to the old-growth forest.

Two additional transplant experiments were conducted in order to identify any differences in annual growth rates of *P. berberina* and *P. flavicans* depending on stand or tree age. For this, transplants of *P. berberina* were hung on young and remnant tree trunks in a post-fire stand in the high precipitation site of Pto. Blest (Fig. 3). Growth increase was checked after one year (2001). The following year, *P. berberina* and *P. flavicans* transplants were hung on tree trunks in a young and an old stand in the low precipitation Espejo Lake area (thalli from Pto. Blest). The results of these experiments are not included in Paper **III** but are presented in the results section below.

Paper IV

Living thalli of five lichens species (*Pseudocyphellaria flavicans*, *P. faveolata*, *Nephroma antarcticum*, *Platismatia glauca* and *Protousnea magellanica*) were collected in the austral summer of 2002. Lichen material was set in 20-30 litterbags and returned to the field in a *N. dombeyi* old-growth stand, on 8 February and 31 March 2002. All samples were collected after a 3-month period, taken to the laboratory, oven dried at 30^{o}C for 24 hours and re-weighed. After weighing, the samples were returned to the bags and taken to their original location in the field. This process was repeated seven times during the course of the experiment from March 2002 to October 2003. Decomposition was expressed as mass loss, i.e. the percentage of the original mass remaining after each sampling time. The annual decomposition constant *k* (Olson, 1963) was calculated.

Sub-samples of two to four bags of each of the five lichen species were taken to the laboratory for chemical analysis on four occasions. N and C concentration were analysed separately in lichens and soil for 0.100 g of the samples. The macro-nutrients P, K, Ca, Mg and S were analysed by inductively coupled plasma optical emission spectroscopy (ICP-OES). The quantity of each element was expressed in mg/g or μg/g.

Results and discussion

Lichen distribution and abundance (I-II)

Succession of epiphytic communities with increasing stand age has been suggested by many authors, both for temperate and boreal forests in the northern hemisphere (Yarranton, 1972; McCune, 1993; Sillett, 1995) as well as for the southern temperate *Nothofagus* forests (Kantvilas, 1990; Pereira & San Martin, 1998). I found that epiphytic lichen communities on *Nothofagus dombeyi* and *N. pumilio* in northwestern Patagonian forests change in composition and abundance with stand age and geographic location (**I-II**). For the Valdivian *Nothofagus dombeyi* forest, the preliminary study indicates that epiphytic lichen succession on trunks largely proceeds as follows. Crustose lichens dominate in the first stages of the forest up until around 90 years. Species richness is greatest when the macrolichen component starts to mix with the dominating crustose lichens. This was the case in the 90-year old stand in my studies. In old-growth, foliose and fruticose lichens dominate, and crustose species are of little importance on tree trunks. Old-growth forests have higher macrolichen species richness (**I**-**II** and Fig. 4). However, the crustose lichen component is mostly found on the younger smooth-bark trees and higher up in the canopy, as found on fallen branches and trees after storms. These results are similar to those found for *N. alessandri* in Chile, where in the same stand young trees have a higher proportion of crustose flora than old ones (Pereira & San Martin, 1998). Vertical change in species distribution in old-growth *Nothofagus* forests was also shown in Tasmanian forests where pioneer species during tree aging were displaced to younger branches and twigs (Kantvilas, 1990).

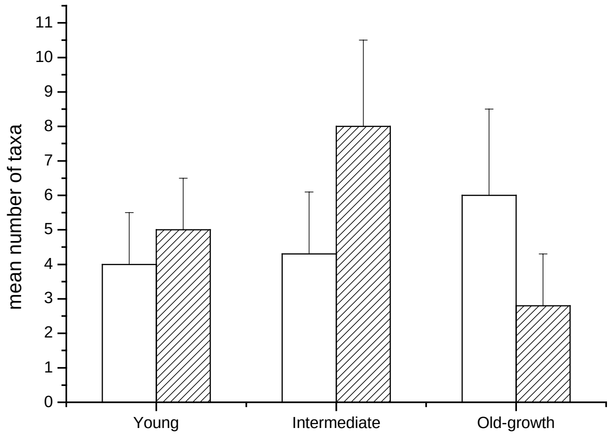

Fig. 4. Mean frequency (SD) of lichen morphospecies richness in three different age class *N. dombeyi* stands in Pto. Blest. (60, 90 and >150 y of age). White bars indicate macrolichens and hatched bars indicate crustose lichens.

I found no differences between north and south exposure of the trunks in terms of either species richness or abundance. Only Pto. Blest, a high precipitation site, showed a greater abundance in the southern (darker) side. The lack of a generally higher abundance on the shadier side of the stems is surprising, since it is commonly claimed that water-demanding species are mostly confined to the shaded part of the trunk. It is possible that the dense structure of younger *Nothofagus* forests and the thick understorey of bamboo might influence this pattern by creating a more homogeneous light and humidity distribution in the lower parts of the trunks (**I**).

Due to the lack of a complete lichen list and keys for identification, especially on the crustose component, the study continued by focusing on the macrolichen flora, in particular on three of the most abundant genera in the region, *Pseudocyphellaria*, *Sticta* and *Nephroma*. All these species have a cyanobiont as the photosynthetic partner, either as primary photobiont or in cephalodia, and so have an important functional role for the ecosystem (Galloway, 1988; White & James, 1988).

Annual precipitation

Macrolichen diversity and abundance showed a general increase with humidity (**I-II**). This relationship was especially clear for *Lobariaceae* and *Nephromataceae* on *N. dombeyi* and *N. pumilio* (**I**). The importance of humidity for abundance and diversity was also reported by Galloway from Chile (1992b) and Nash and Moser (1982) from the USA. The increase of macrolichen richness in the litterfall with humidity can partly be explained by the presence of low precipitation site species higher in the relatively drier tree crowns in high precipitation sites, which adds to the specific flora of these habitats (Pike *et al.*, 1975). The positive effect of increasing precipitation on lichen biomass (**I-II**) may largely be attributed to longer coherent periods of growth in high precipitation sites, whereas the low precipitation sites might suffer from extended dry periods when lichen thalli cannot photosynthesise (Hauck & Meissner, 2002; Dahlman & Palmqvist, 2003).

The average biomass in the old-growth stands in this study (2-20 kg ha $^{-1}$, being highest in the *N. pumilio* stand in Puyehue, lies in the same range as that reported from studies on epiphytic lichen litter in temperate coniferous forests of the northern hemisphere (McCune *et al.*, 1997; Dettki & Esseen, 1998; Price & Hochachka, 2001). In boreal forests, a considerably greater lichen biomass has been reported (Esseen, 1985). Unfortunately, there are no estimates of the relationship between lichen litterfall biomass and standing biomass for *Nothofagus* forests, unlike the ones found for the northwestern USA where the relation is approximately 1/100 (McCune, 1994).

Stand age

Stand age influenced epiphytic macrolichen abundance and diversity (**I-II**), which confirms results from other parts of the world (Lesica *et al.*, 1991; McCune, 1993; Dettki & Esseen, 1998; Boudreault, Gauthier & Bergeron, 2000; Price & Hochachka, 2001). For many lichen species, old-growth stands provide more suitable microhabitats. Young or managed stands have a narrow spectrum of microhabitats for lichen establishment and younger, less abundant populations of the relatively slow growing lichens. Furthermore, poor dispersal of epiphytic lichens may delay recolonisation of secondary stands (Sillett *et al.*, 2000).

In general, patterns of abundance of different functional groups showed relatively small changes with stand age (**II**). One trend was that the relative importance of the genus *Pseudocyphellaria* increases with stand age. However, there was no relative increase of Fruticose lichens with stand age in this study sites, unlike results reported from western USA and Canada (McCune, 1993, Price & Hochachka, 2001) (Fig. 5). Species of the different functional groups start to colonise secondary *Nothofagus* stands more or less simultaneously (**II**).

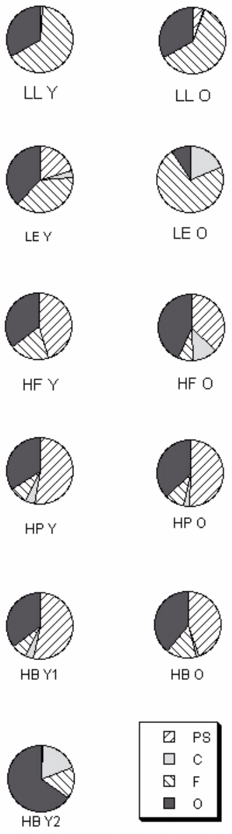

Fig. 5. Biomass proportion of the lichen functional groups found in litterfall in the different young and old stands of *N. dombeyi.* (Ps: Green *Pseudocyphellaria* spp.; C: Cyanolichens; F: Fruticose lichens; O: Other green lichens)

Cyanolichens have been reported to be strongly associated with old-growth forest (McCune, 1993; Kuusinen, 1994; Kuusinen, 1996; Neitlich & McCune, 1997; Hedenås & Ericson, 2000). In European boreal forests the presence of cyanolichens in old forests is more marked in humid habitats and related to broadleaved tree species (Kuusinen, 1994), a pattern which might be explained by the greater water requirements of cyanolichens (Nash III, 1996b). In my study, the positive effect of increasing precipitation and age is more pronounced for green *Pseudocyphellaria* spp. (tripartite lichens) and other green foliose lichens than for bipartite cyanolichens (**I**-**II**).

In northwestern USA it has been shown that remnant trees in young stands may act as sources of propagules for the establishment of lichens on the surrounding younger trees (Peck & McCune, 1997; Sillett & Goslin, 1999). In my study, both species richness and abundance varied greatly between plots in young stands, but showed a trend towards increased diversity and abundance near remnant trees and in smaller stands (**II**). The dispersal abilities of the studied species are unknown. Some species may be able to spread quickly but no direct studies have been carried out on southern hemispheric taxa (Kantvilas & Jarman, 2004). Thus, research is needed on whether regional rarity of species is related to their dispersal strategy.

Growth and decomposition (III-IV)

*Growth pattern (**III**)*

The use of lichen pendants for measuring growth rates (McCune *et al.*, 1996) proved to be a reliable method for estimating biomass growth of *P. berberina.* Growth increment in *P. berberina* transplants was independent of whether it was hanging freely or attached to trees. Mean annual growth increment for *P. berberina* varied between 9% and 15%. These results are comparable to similar experiments on northern hemisphere *Lobariaceae*, which have shown annual growth rates of between 8% and 30% (Denison, 1988; Sillett, 1994; McCune *et al.*, 1996; Muir, Shirazi & Patrie, 1997; Sillett & McCune, 1998; Brown & Dalton, 2002). To a large extent, variation in annual lichen growth increment depends on year-to-year differences in climate (Brodo, 1965). This was probably also the explanation for the inter-annual differences in growth of *P. berberina* found in study **III**.

Growth showed a strong seasonal variation. *Pseudocyphellaria berberina* grew most in winter. This pattern might be explained by high winter precipitation in the form of rain or snow, and temperatures that do not inhibit photosynthesis.

Growth in relation to stand and tree age

The additional growth experiments suggest no influence of either stand or tree age on the growth rates of lichen transplants. In the Espejo area, lichen transplant growth in young and mature stands showed no significant differences (T-test, P=0.12). Similarly, no differences in growth between young and remnant old trees in the same stand could be detected (T-test, P= 0.59; Fig 6). *Pseudocyphellari berberina* in particular is found less often in the Espejo area (I-II). The discovery of lack of differences in growth rates supports the hypothesis that dispersal is the limiting factor for the distribution of this species (Sillett *et al.*, 2000; Hilmo & Såstad, 2001).

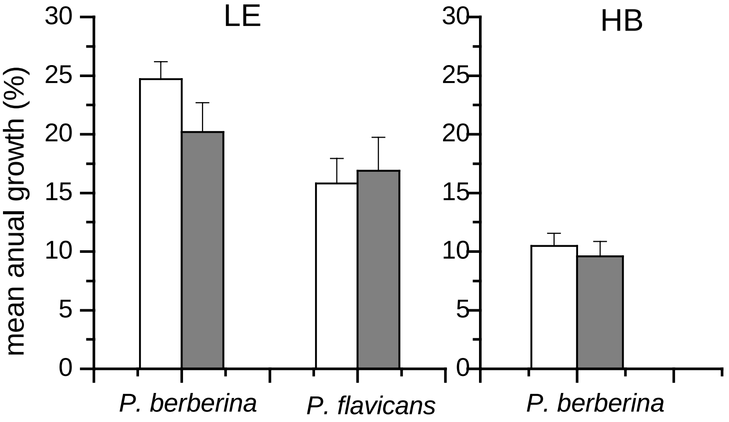

Fig 6. Mean annual growth (SD) of *Pseudocyphellaria berberina* and *P. flavicans* in: LE Espejo area and HB: Pto. Blest. White bars indicate young and filled bars indicate mature stand and tree, respectively.

In all experiments, the overall effect of the donor thallus on transplant growth was very weak except during the first season after transplantation; this subsequently disappeared suggesting that the lichens had acclimatised to the new habitat conditions (III). A similar effect was reported for *Lobaria oregana* and *Pseudocyphellaria rainierensis* (Sillett, 1994): thalli taken from the forest edges where the transplants were acclimatised to previous conditions did not grow well. The effect of donor thalli is small as long as they are all taken from the same area.

Decomposition (IV)

Decomposition rates vary greatly among different lichen species (Wetmore, 1982; Guzman, Quilhot & Galloway, 1990; McCune & Daly, 1994; Esseen & Renhorn, 1998). In general, fruticose lichens have a much faster decomposition rate than foliose species due to the high area/volume ratio, which facilitates rapid decomposition and leaching of cellular components (McCune & Daly, 1994; Esseen & Renhorn, 1998; Coxson & Curteanu, 2002). I found lower decomposition rates on the tested lichen species than were found in previous studies (McCune & Daly, 1994; Esseen & Renhorn, 1998). However, the *Pseudocyphellaria spp.* decomposition rates in my studies were comparable to similar studies in the Chilean part of the Valdivian forest (Guzman, Quilhot & Galloway, 1990). Decomposition rate was highest after the winter and spring seasons, and lowest after the autumn.

I also found that nitrogen content varied greatly between species. *Pseudocyphellaria faveolata*, *P. flavicans* and *N. antarcticum* contain nitrogen-fixing cyanobacteria, and had nitrogen concentration that was three times greater, and had a lower C/N ratio, than *P. glauca* and *P. magellanica* (**IV**). In other studies, higher decomposition rates were observed in lichen species with greater N content and low C/N ratio, and decomposition rates were especially higher in nitrogen-fixing lichens than in non-fixing (Crittenden & Kershaw, 1978; Guzman, Quilhot & Galloway, 1990). In this study, however, *Pseudocyphellaria* and *Nephroma* species had the lowest decomposition rates. After nitrogen, phosphorus (P) is the mineral nutrient most demanded by decomposers, making the initial content of this element quite important in determining the decomposition rate. *Pseudocyphellaria* species had the highest initial values of P, though these were the species that decomposed slowest.

Lower decomposition rates might be due to chemical compounds inhibiting decomposition (Wetmore, 1982; McCune & Daly, 1994; Gauslaa, 2005). Abundance of *Lobariaceae* in the Valdivian forests (**I-II**) constitutes a significant protein resource for the herbivorous fauna (**IV**) (Galloway, 1991). However, the fact that just these lichens have slowest decomposition rates in spite of high levels of N and P, and are seldom consumed by herbivores, suggests the presence of an effective anti-herbivore system (Galloway, 1991). Secondary metabolites in the form of triterpenoids could be responsible for this (Galloway, 1995).

Greater mass loss after the first season occurred for lichens placed in early summer compared to those placed in early autumn. This might be due to a positive effect of high summer temperature during the initial phase of decomposition. Otherwise, lichens mainly decomposed in winter, as has been shown in other studies (Moore, 1984; Taylor & Jones, 1990; Coxson & Curteanu, 2002). Frequent freeze-thaw cycles might be the most important factor that accelerates decomposition (McBrayer & Cromack, 1980).

The growth form was proved to influence the element concentration of lichens, as foliose lichens had higher content of the majority of elements compared with fruticose lichens (St Clair *et al.*, 2002). This can partly be attributed to foliose lichens absorbing substances originating from the surface of the bark more easily. Accumulation of certain minerals might consequently depend on the morphology (Brown, 1991). A more upright structure, such as that of *Platismatia glauca*, may favour the uptake of dust and elements from wind and canopy leached particles. This is especially seen in the concentrations of Al, Fe, Na, Si, and Ti, which can all be expected to derive from soil dust (Caldiz, unpublished results). In all the other lichens, these elements increase strongly during the decomposition period, suggesting contamination from soil.

Nitrogen, lichens and Nothofagus forests

Using the results from Papers **I**, **II** and **IV**, I made a rough calculation of the quantity of nitrogen provided by lichens to the different *Nothofagus* stands (Fig. 7). For *N. dombeyi* forests, it is remarkable that in high precipitation sites, especially in the old-growth stands, the amount of nitrogen in the litter is around 200 g ha^{-1}, while in the low precipitation sites it is less than 30 g ha^{-1}. The major sources of nitrogen to the ecosystem among the lichen tested are the green *Pseudocyphellaria* species, giving more than 50% of the total amount in old-growth stands. Bipartite cyanolichens are not a major source of nitrogen in any of the cases, probably because so few of these lichens were found in the litterfall. Fruticose species are always a minor nutrient source.

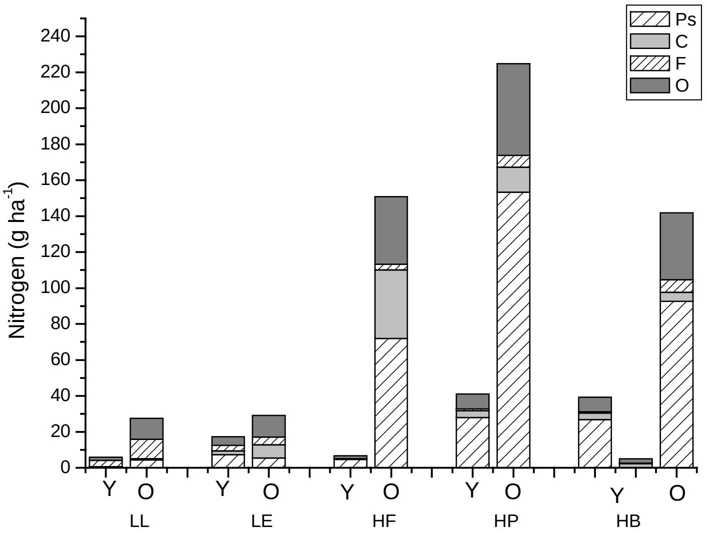

Fig. 7. Estimated amounts of nitrogen in litterfall of different functional groups for the studied *N. dobeyi* stands. Note differences between old-growth and young stands, especially in the high precipitation sites. (Ps: Green *Pseudocyphellaria* spp.; C: Cyanolichens; F: Fruticose lichens; O: Other green lichens)

Conclusions

Gradients in biomass and species diversity of northwestern Patagonian epiphytic macrolichen communities are positively correlated to increasing annual precipitation. This is especially clear for the cyanolichen species of the genus *Pseudocyphellaria*.

Lichen biomass and diversity increases with stand age but colonisation of young stands is probably also influenced by the presence of remnant old trees and the distance to old-growth forest. In old-growth forests, the nitrogen input by N-fixing cyanolichens can be significant, mostly due to the abundance of tripartite *Pseudocyphellaria* and *Nephroma* species rather than bipartite species.

Surveys of trunks and litter provide supplementary information. However, future studies should also include surveys of branches and/or canopy in order to provide representative information on lichen abundance and diversity.

Growth and decomposition showed a similar seasonal pattern, with highest rates recorded during winter for all macrolichens analysed. Constantly humid conditions may favour both processes during the winter season.

Annual growth rates of *Pseudocyphellaria berberina* showed a 10-20% increase in biomass. No differences in growth rates were found in relation to transplanting method, phorophyte age or stand age. I conclude that limitations in dispersal or establishment are more important than stand microclimate for performance of *P. berberina* in post-fire stands.

Cyanolichens with highest nitrogen content showed the lowest decomposition rates, contrary to what was expected. This supports the hypothesis of the presence of an anti-herbivore component in the *Lobariaceae* family in southern temperate forests.

Post-fire sequences are well suited to study the effects of disturbance on lichen distributions in *Nothofagus*. Further studies are needed to analyse the effect of gap size and remnant trees on recolonisation of epiphytic lichens. Such information will be essential to predict the impact of the forestry on previously undisturbed forest landscapes.

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