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Ecology of bryophytes along altitudinal and latitudinal gradients in Chile

Studies in austral temperate rain forest bryophytes 16.

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Abstract: The bryophyte vegetation in twenty-eight hectare plots in forests of S-Chile between 38° and 42°S and sea level and the forest line has been studied. Since bryophytes are fully dependent on atmospheric water and nutrient supply, they are good indicators of ecological conditions, especially for humidity. Therefore cover of epiphytic bryophytes, percentage of hepatics, composition of life forms and phytomass of epiphytic bryophytes were used as parameters. Cover and phytomass of epiphytic bryophytes as well as percentage of hepatics show moderate values in the lowlands, peak values in the montane belt (400-800m) and low values in the high montane to subalpine forests. This zonation corresponds with the composition of life forms and is attributed to a higher humidity in the montane belt. Life forms characteristic for the lowlands and submontane belts are pendants, those for the montane belt are wefts and tails, and those for the high montane and subalpine belts are mats and cushions. The same zonation is found in New Zealand at comparable latitudes. The altitudinal differences are much stronger than the latitudinal ones. Compared with similar transect studies in New Zealand, there is a comparable zonation based on bryophytes. The percentage of hepatics as a good indicator of humidity, is – both in Chile and New Zealand - higher in the transects along the coast with higher precipitation, lower in transects in the inland with less precipitation, and increasing with altitude. Compared with tropical rain forests, the “mossiness” of temperate rain forests expressed by phytomass of epiphytic bryophytes per hectare, cover and percentage of hepatics is comparable to tropical rain forests above 2000 m, which is the corresponding elevation with regard to the mean annual precipitation. In Chile, however, there is a distinct decrease of “mossiness” in the high montane and subalpine forests, which is attributed to special climatological conditions, whereas bryophytes reach maximum cover and phytomass in the tropical high montane and subalpine forests. A comparison with montane forests in Europe in 48°N reveal, that phytomass and percentage of hepatics is distinctly less than in the true rain forests of the southern hemisphere.

1. Introduction

The temperate rain forest of the southern hemisphere in New Zealand, Tasmania and Chile, although thousands of kilometres separated from each other, are parts of the same austral floristic realm. The geological background is that these regions were parts of the Gondwana continent and remained after the separation of continents in a cool temperate climate since 82 mio years. By this way, the aspect of the late cretaceous vegetation with its archaic gymnosperm flora and primitive angiosperm flora was preserved.

Within the Bryoaustral-project, attempts are made to study the ecology, phytogeography and taxonomy of austral temperate rain forests with special reference to a comparison of the bryoflora and –vegetation of New Zealand and southern Chile and with regard to the geological background that both regions were formerly connected. Bryophytes play a special role in this respect, because they are phylogentecially much older than phanerogams. This is expressed by the fact that the phanerogamic flora of both regions is only related on a genus level (Wardle et al. 2001), but the bryophyte flora of Chile and New Zealand has many species in common. Amongst mosses, 176 species are identical in both parts (Beever 1999)

The reason for the good floristic comparability of New Zealand and southern Chile is – beside of the common geological history - the presence of temperate rain forests in both regions, which is a result of their location in comparable latitudes (38° - 47°S) resulting in a similar climate, which persisted more or less since the separation of the Gondwana continent (in contrast for example to India or Australia, which drifted into different latitudes and have undergone severe climatic and also floristic changes).

Temperate rain forests cover still 7,6 mio hectares in Chile. Eighteen percent of this area are preserved as national parks. They are classified in

1. the Valdivian rain forest (Zone X) between 37°45' S and 43°20' S,
2. the Patagonian rain forest (Zone XI) from 43° 20' S to 47° 30' S, and
3. the Magellan rain forest (Zone XII) south of 47° 30'.

Aim of this study was

(a) to register the characteristics of the bryophyte vegetation of temperate rain forests in southern Chile,

(b) to determine and interpret the variation of parameters along latitudinal and latitudinal gradients, and

(c) to compare the bryophyte vegetation of temperate rainforests in southern Chile with those from New Zealand.

The Magellan rain forest has no correspondence in New Zealand and his therefore omitted here from this survey; the Patagonia rain forest is largely inaccessible by roads. It is situated in the part of Chile which is splitted into numerous islands. Therefore the study was based only on the Valdivian region. There, however, spurs of the Patagonian and Magellan rain forest are found at higher elevations.

Bryophytes are excellent indicators for climate, specially humidity, to a lesser extend also for temperature and light. They can therefore be used for characterizations of habitats and the elaboration of zonations. Reason for the utilization as humidity indicator is that especially epiphytic bryophytes fully depend on atmospheric nutrient and water supply. The amount of precipitation is mainly responsible for the nutrient supply. Therefore the phytomass of epiphytic bryophytes depends on precipitation but is modified by the length of turgescence period at daylight, which determines the length of phytosynthetic period. Bryophytes can therefore be used all over the world as sensitive indicators for the humidity of a habitat. Special mechanisms for adaptation to humidity are life forms (especially pendants as indicator for fog, wefts, tails and fans for hyperhygric conditions, mats and turfs for mesic conditions and cushions for habitats with extended dry periods), as well as morphological and anatomical adaptations for water uptake and water storage. The humidity is not equal to precipitation but includes also mist, frequent high relative humidity, dew or frequent cloud layers. Bryophytes are so sensitive that microclimatic differences (for example slopes of different expositions, depressions, ridges, valleys) are expressed. The effect of temperature is not that important for bryophytes. Although

photosynthesis is doubled by 10°C, the higher temperatures result in a higher transpiration and a lower relative humidity. Low temperatures in humid climates, however, can result in longer periods with high relative humidity, as for example at higher elevations in mountains, causing a high mossiness. Light is the less important factor due to the low compensation point of bryophytes. It allows to separate bryophyte vegetation into light and shade synusiae.

2. Methods

Field work was carried out in February and March 2001. Altogether 28 hectare plots were studied in forests at different elevations (tab. 1), usually in altitudinal intervals of 200 m and also 100 m along transects from the lowland to the forest line between 38° and 42°S. The hectare plots were chosen in homogeneous forest sites, which gives a good base for comparability. In a few cases two hectare plots in the same altitude were studied, which provides a chance to determine the amount of variation between hectare plots at the same elevation. The location of the study areas is given in the appendix, the location of the transects is given in fig. 1. With the exception of 42°S and in contrast to some transects studied in New Zealand, the transects start at 400 m which is due to the fact that the regions below 400 m are cultivated. All study areas with the exception of the relevés 12-14 are situated within national parks which is a guarantee for almost undisturbed situations.

As in the study on the ecology of rain forests bryophytes of New Zealand (Frahm & Ohlemüller 2001), the following parameters were registered in the field:

1. Percentage of cover of bryophytes on the ground and on trees.

2. Life forms are expressions of morphological adaptations to ecological conditions. Thus life form spectra from various elevations or latitudes reflect the response of bryophytes to varying ecological parameters such as precipitation, fog, air humidity, length of dry or humid periods or

dry and wet seasons. An advantage of these life forms is that all ecological parameters are integrated.

As in previous studies (Frahm 1990a, 1994, Frahm & Ohlemüller 2001), the following life forms were distinguished:

Tails (e.g. *Schistochila*, some species of *Plagiochila*, *Schimperobryum*, including fans e.g. *Lopidium*)

Wefts (e.g. *Teleranea* spp., *Lepidozia* spp., *Lepicolea* spp. *Trichocolea* spp.)

Mats (*Bazzania* spp., pleurcarpous mosses, creeping acrocarpous mosses such as *Stenotrichum* spp., creeping hepatics such as *Frullania*)

Turfs (*Dicranoloma* spp., *Herbertus* spp.)

Pendants (*Weymouthia* spp.)

Dendroids (better dendroid turfs, since dendroid is a growth form, e.g. *Dendroligotrichum*, *Porothamnium*, including umbrella mosses such as *Hypopterygium*)

Cushions (e.g. *Leptostomum* spp., *Lepyrodon* spp.)

Life forms were determined only from epiphytic bryophytes, because they are most dependent on atmospheric factors. The best indication of the value of life forms is the fact that the same species can have different life forms under different ecological conditions. For example, species of *Weymouthia* can form creeping mats under less humid conditions but pendant beards under humid conditions.

3. Phytomass of epiphytic bryophytes per m² and hectare.

Phytomass per m² (wet weight) was determined by scratching off all bryophytes from 0.5 m² on a tree trunk and weighting with a balance. Next it was estimated how many times this bryomass was growing on the tree and how many trees were on 20x 20 m, from which the weight in kg/hectare was calculated. The measurements/estimations was 2-3 times repeated and varied by 10-20%.

4. Percentage of liverworts as an indicator for the humidity of the relevée.

In addition, measurements of the relative light intensity in the forests, estimations of tree height and tree girth and canopy cover were made,

Tab. 1: List of hectare plots studied along altitudinal and elevational gradients.

38°S	Parque Nacional Conquillo	
	1200	
1400		
1600		
39°S	Parque Nacional Huerquehue	900
1000		
	Volcan Villarrica	1100
1330		
1450		
40°S	Parque Nacional Puyehue	200
325		
500		
700		
850		
950		
1050		
	Cordillera Pelada	600
41°S	Laguna Sargazo	400
	Volcan Calbuco	600
700		
800		
900		
1000		
1100		
42°S	Region Hornopiren	10
20		
30		

which are here not taken into account.

Comparative measurements of the temperature and especially air humidity as in New Zealand (Frahm & Ohlemüller 2001) were not performed because the reviewers of the German Research Foundation did not consider this topic as important.

3. Results

3.1 Cover

The cover of bryophytes on the ground has been omitted from the evaluation, because it is too much influenced by the geology (percentage of

rocks, forests on lava flows), forest structure and composition of herb and shrub layer, especially the presence of *Chusquea*, which cover large uniform masses on the forest floor.

The cover of epiphytes is not only influenced by precipitation but humidity that means also by the microclimatic situations and is higher in valleys with streams and on different expositions. Eastern slopes are generally more humid than western slopes. Nevertheless there is in general a trend (Fig. 2) that the forests in S-Chile have moderate covers of epiphytic bryophytes (20-40%, locally also less) below 300 m but a sudden increase to 75-90% in elevations between 300 and 800 m and a sudden decrease above 900 m to 20%

followed by a gradual decrease towards the forest line with only 1% of epiphytes. At high montane and subalpine elevations, the epiphytic bryophytes are replaced by lichens. A change from epiphytic bryophytes to epiphytic lichens can be observed in many parts of the world, either on different trees in the same region or in different parts of the tree (bryophytes on the trunk, lichens in the crown). According to unpublished results obtained in Central Europe, "lichen trees" differ from "bryophyte trees" by the length of the period, during which the plants are turgescens ($rH > 80\%$). Thus epiphytic lichens are much more drought resistant than epiphytic bryophytes and indicate drier conditions.

3.2. Life forms

Life form spectra are generally characteristic for different ecological conditions. These can be different altitudinal belts but also different microclimatic habitats. The latter is expressed by differences in life form spectra at the same altitude in different habitats (valleys, slopes, different expositions). Pendants are generally significant in foggy areas (indicators of frequent cloud layers) but on a small scale in places near rivers or streams. The evaluation of all study areas in different altitudes and latitudes (tab. 1) reveals:

1. the lower elevations (< 400 m) are characterized by high percentages pendants (in Chile only *Weymouthia mollis* and *W. cochleariifolia*; but can occur together, an ecological differentiation seems impossible).
2. the elevations from 400 – 900 m are characterized by a dominance of tails (incl. fans) and wefts reflecting the high air humidity. Turfs and mats are represented with low percentages. Pendants can be found but only in special habitats.
3. Above 900 m, cushions (*Lepyrodon*, *Leptotrichum*) and mats (*Hypnum*, creeping mosses such as *Stenotrichum* or creeping hepatics such as *Frullania*) are dominating.

3.3 Phytomass of epiphytic bryophytes

Although these values are obtained with a relatively rough method, they give reasonable results as shown by comparison of measurements obtained in the same hectare plot or in different plots in the same region at the same elevation.

The results varied no more than 20%. The values of "bryomass" give a very vivid ideas of the "mossiness" of a region, which seems to be directly related to the humidity of a habitat.

The phytomass of epiphytic bryophytes is moderate at sea level. Three calculations in the Hornopirén region at 42°S revealed values between 480 and 600 kg/hectare wet weight. The amount is double as high at 400 m and then raises in the Calbuco-transect (41°S) and the Puyehue-transect (40°S) to maximum values of around 5000 kg/hectare in 700 – 800 meters elevation. This maximum is correlated with frequent cloud layers in this altitude, which could be observed especially in the morning hours. Above 800 - 900 m there is a sudden decrease to 100 – 250 kg/ha, values < 100 kg in 1300 – 1400 m and a minimum at the forest line. An exception are the elevations in 1100 and 1300 m at Volcán Villarica, where few but heavy cushions of *Leptostomum* revealed higher values.

The wet weight of phytomass of epiphytic bryophytes gives also an approximation of the water storing capacity, since the wet weight is around three times as high as the dry weight (Frahm 1990a, 1994). The calculation of the water storing capacity over a period of time (month, year) is, however, misleading, because it is based on the assumption that epiphytic bryophytes have this water storing capacity all the time. This is not the fact when they are wetted. The more humid the habitat is, the less water is stored because the bryophytes do not dry up in between. Furthermore, this calculation does not regard the interception water. It has to be considered that the different life forms of bryophytes can store different amounts of interception water. Cushion have a high, turfs a medium amount of interception water and tail and fans have almost no interception water. The wettest sites are, however, characterized by a dominance of tails and turfs.

3.4 Percentage of liverworts

The percentage of liverworts (fig. 4) is correlated with the values for the phytomass of epiphytic bryophytes (fig. 3). This means that liverworts count for the high phytomass values. It is also an expression of the humidity. Higher amounts of

mosses in lower elevations and low percentages of liverworts between 5 and 20% indicate longer dry periods, which many hepatics cannot stand. Above 400–500 m, the bryophyte vegetation is dominated by liverworts, and in some altitudes (Calbuco 700–800 m), liverworts count for 90–95% of the bryophytes. Like the phytomass values, liverwort percentages drop dramatically above 800 m at 40–41°S or 900 m at 39°S to 10% and less.

3.5 Altitudinal zonation

The data for epiphyte cover (fig. 2), percentage of hepatics (fig. 4) and phytomass of epiphytic bryophytes (fig. 4) have all the same trend: moderate values in the lowlands, peak values 400–800 m and low values above 800 m. This can be interpreted as direct expression of the humidity, whereby the humidity does not only mean high precipitation but also frequent cloud layers, a phenomenon, which can be especially observed during the morning hours.

All three parameters are an expression of mainly the same factor: humidity. Only humidity has an uneven distribution along an altitudinal transect, whereas temperature has an even decrease by 0.6°C/100 m elev. Thus bryophytes as an expression of different humidity regimes allow to differentiate the following altitudinal zones in southern Chile between 38° and 42°S :

<100	lowland belt
100- 400 m	submontane belt
400 – 800	montane belt
900 – 11-1300	high montane belt
11-1300 - forest line	subalpine belt

The limits vary depending on the latitude and the substrates (lava flows). Especially the change high montane – subalpine varies between 1100 m (41°S, Calbuco transect) and 1500 m (38°S, Conquillo transect).

The **submontane belt** consists of forests with *Eucryphia* (“Eucryphietum”), *Drymis winteri*, *Laurelia* and *Weinmannia*. It is bryofloristically not much different from the montane belt and has many species in common. Species confined to these lower elevations are the mossballs of *Rigodium implexum*. The forest is characterized

by moderate cover of epiphytic bryophytes (20–40%), and accordingly moderate phytomass (<600 kg/ha) and a moderate percentage of hepatics (<20%). The ecological characterisation is thus humid but not as humid as the montane belt.

The **montane belt** extends to 800 m at 40° and 41°S but to 900 m at 39°S. This “bosque siemprevverde” is composed by conifers such as *Saxegothea*, *Podocarpus* or *Fitzroya* but also *Nothofagus dombeyi*, *N. betuloides* and *N. nitida*. Characteristic bryophytes of the forest below 900 m are *Hypopterygium arbuscula*, *H. didictyon*, *Weymouthia mollis*, *W. cochleariifolia*, *Monoclea forsteri*, *Lopidium concinnum*, *Schimperobryum splendidissimum*, species of *Plagiochila*, *Schistochila*, *Lepidolaena*, *Bazzania*, *Rhizogonium*, *Teleranea*, *Poroathamnum*, *Trichocolea*, *Lepicolea*, *Lepidozia*, *Lepidolaena*, *Herbertus*, *Ptychomnion*. It resembles the high montane forest in the northern Andes. Bryological characteristics are high cover of epiphytic bryophytes (75–90%) and accordingly a high phytomass (2000–5000 kg/ha) and a high percentage of hepatics of 40–50%, with peak values in extreme humid situations of 80–95%.

The **high montane belt** consists of *Nothofagus (pumilio, oblique, alpina)* forests above 900 m between 38° and 42°S resembles the subantarctic forests at 51°S (Punta Arenas) at low elevations. They consist both of *Nothofagus pumilio* and share the same floristic elements of the Magellan Forest such as species of *Lepyrodon*, *Zygodon*, *Stenotrichum*, *Leptostomum*, *Frullania*., *Dicranoloma*, *Eucamptodon* and *Orthotrichum* on trees, in more humid situations also *Lepicolea*, and “*Austrofossombronia*” spp., *Bartramia* spp., *Breutelia* spp., *Bryum* sect., *Rosulata*, *Bartramidula* spp. and *Dicranoloma* spp on ground. It resembles the high andine *Polylepis* forests of the equatorial latitudes by the presence of genera and species of *Lepyrodon*, *Breutelia*, *Ditrichum*, *Symphyogyna* but has also austral elements such as species of *Schistochila*, “*Austrotortula*”, *Leptostomum* and *Dicranoloma*. The epiphytic species can also be found at lower altitudes but either in the canopy or in special habitats (wind swept ridges). The

high montane forest has a low cover of epiphytic bryophytes of 5-10%, even lower than in the submontane belt, with accordingly low phytomass values (20-70 kg/ha) and a percentage of hepatics of 5-10%.

The **subalpine belt** is situated above 1100 m (41°S) and 1400 m (38°S). It is characterized by an extrem low epiphyte cover (1%) on dwarf trees of *Nothofagus antarctica* and *N. pumilio* and accordingly low phytomass values as well as low percentages of liverworts (1-5%). It has also extreme low species diversity. Epiphytes consist of *Hypnum* sp. and *Dicranoweisia* sp., which represent life forms of mats and cushions. The low epiphyte values of 1% cover and 5kg/ha are in striking contrast to the better light conditions at higher altitudes. Hepatics count for 5% or even less.

4. Discussion

4.1. Comparison with New Zealand

The location of the transects studied in New Zealand (Frahm & Ohlemüller 2001) are almost directly comparable with those of the present study in Chile (cf. tab. 2), only the southernmost transects in New Zealand have no resemblance in Chile.

The percentage of liverworts in New Zealand was distinctly correlated with the different precipitation along the different transects. This phenomenon can also be observed in Chile, where the Calbuco transect (41°S, close to the ocean) has higher liverwort ratios than the Puyehue transect (40°S, more distant from the ocean). The precipitation at 41°S in Chile is 3300 mm/year at lower elevations and 4500 mm at higher elevations, resulting in a percentage of liverworts between 40 and 90%. These values are comparable to the Haast-transect (South island of New Zealand, 44°S) with precipitation of 3500 mm at sea level and accordingly higher values at higher altitudes. We have also in increase of the percentage of hepatics with altitude in the temperate rain forests in New Zealand and Chile.

The effect that cover of epiphytic bryophytes, phytomass and percentage of hepatics decreases dramatically above 800-900 m elev. in Chile cannot be realized along all transects in New Zealand, where we found peak values at 800 – 1000 m elev. in the transect along the coast of the South Island and 1200 m at the Urewera transect in the North Island and only decreases at the St. Arnaud transect and Ruapehu transect. Although New Zealand and southern Chile are included in the same type of climate (Troll & Paffen in Blüthgen 1966), the climate is not identical as expressed by the differences in the bryological parameters analyzed in both regions. Wardle et al. (2001) in their “Comparison of the flora and vegetation of the southern Andes and New Zealand” (which means the phanerogamic flora and vegetation) give curves for temperature and rainfall for pairs climate stations in New Zealand and Chile. The curves show that temperatures (calibrated to the same latitude and altitude) are very similar although in average lower in Chile, which is attributed to the cool Humboldt current. Precipitation, however, a factor much more important for bryophytes, differs in the way that the values for the months October to April are generally much lower in Chile. This means that the climate in New Zealand is perhumid but has a short dry season in Chile during summer (fig. 5).

The life forms spectra in Chile are comparable to those in New Zealand with the exception that dendroids play not that role in Chile as in New Zealand. There are only few species in Chile (*Hypopterygium arbuscula*, *Dendrologotrichum dendroides*) and were rarely found in our relevés.

4.2 Comparison with the tropics

Generally temperate rain forests are distinguished from tropical rain forests by the lack of vascular epiphytes. An interesting question is whether and if, how temperate rain forests are distinguished from tropical rain forests in terms of their “mossiness”. Generally, the amount of bryophytes in tropical rain forests expressed by phytomass is lowest at sea level (1kg/ha in Borneo) and still low below 2000m (<20 kg/ha in Borneo and 44 kg/ha in Zaire, Frahm 1990a,

	38°S	39°S	40°S	41°S	42°S	43°S	44°S
New Zealand	Urewera	Ruapehu	St. Arnaud, Karamea		Glacier	Franz Josef	Haast
Chile	Conquillo	Huerquehue, Villarrica	Puyehue	Calbuco	Hornopirén		

Tab. 2. Location of study areas in New Zealand and Chile

1994). The values increase above 2000 m alt. and reach a maximum of 1300 kg/ha in Borneo and 6000 kg/ha in Zaire at the forest line. The relations are different in temperate rain forests. Although the amount of precipitation is comparable, the temperatures are different because of the different latitude. However, high temperatures together with low light intensities result in a reduction of the net-photosynthesis of bryophytes (Frahm 1990b). Therefore the phytomass values starts with comparably high values at sea level and raise with elevation with increasing humidity (precipitation, cloud layers). Phytomass starts with values of 200 – 400 kg/ha dry weight in Chile below 400 m elev., reaches 600 – 1700 kg/ha dry weight between 500 and 900 m but decreases to 2 kg/ha dry weight at the forest line. The 200 – 1700 kg/ha dry weight in Chile between sea level and 900 m are thus comparable to elevations between 2000 and 3300 m in equatorial latitudes.

The fomula proposed by Pócs (1980) from studies in Tanzania, that the phytomass of epiphytes per hectare in kg is equivalent to the precipitation in mm exceeding 100 mm, could not be confirmed for Chile, neither for Borneo (Frahm 1990a) nor for Zaire (Frahm 1994). In New Zealand, only determinations of the phytomass per m² were made (Frahm & Ohlemüller 2001). It is probably an accidental result similar to the effect that the phytomass of epiphytic bryophytes in g/m² sometimes resembles that in kg per hectare.

The resemblances of phytomass in tropical and temperate rain forests is almost in accordance with the temperature. The mean annual temperatures in our transects in New Zealand are 8-11°C at sea level in the South Island and 9-10°C at 600 m in the North Island (= 13-14°C

reduced to sea level by 0.6°C/100 m elev.). The range of 8-14°C is found in Zaire at elevations between 2100 and 3400 m elev. (Frahm 1990a). The cover of epiphytic bryophytes with 20-40% below 300 m elev. in Chile is comparable to elevations between 1500 and 2000 m in the tropics (Borneo: Frahm 1990c, Zaire: Frahm 1994). Values of 40-90% in Chile between 400 and 900 m are comparable to elevations between 2000 and 3300 m. The decrease above 900 m in Chile has no resemblance in the tropics, where the cover values reach maxima at the forest line.

In general there are many bryological affinities between rain forests of the austral region as well as tropical regions in the according elevations. This concerns

a. An identical physiognomy expressed by the “mossiness”, which is based on the phytomass and cover of epiphytic bryophytes, similar life form spectra, and varying percentage of liverworts. b. Identical genera and even species in comparable altitudes. The correspondence is sometimes extreme, as in the case of “mossballs”. Such balls occur in humid forests on branches in the canopy and are produced in New Zealand, Central Africa and southern Chile by *Dicranoloma billardieri* or the hepatic genus *Lepicolea* in New Zealand, SE-Asia and southern Chile.

As expressed by the identity of species or genera in the temperate and tropical montane forests, identical life form spectra, phytomass etc., there is practically no difference in the bryophyte vegetation of the temperate and the tropical forests. The main difference is the lack of vascular epiphytes in the temperate forests.

4.3 Comparison with Europe.

A similar climate classification as in New Zealand and Chile is attributed by geographers also to certain parts of Europe. According to Troll & Paffen (in Blüthgen 1966), the climate of the west coast of New Zealand shall resemble that coastal part of S-Chile and also the SW-corner of Ireland and the southern part of the North Island of New Zealand the Valdivian region in Chile and western Europe. Due to the lack of forests in SW-Ireland, there is no comparison possible, however, in the mountains of Central Europe we have also regions with high rain fall (1600 – 2000 mm/yr), which can be compared with the situation at the St. Arnaud and Urewera transects in New Zealand (with 1575 viz. 2050 mm/yr, Frahm & Ohlemüller 2001). Different is, however, the mean annual temperature, which is lower. Frost and snow cover are also possible in the southern hemisphere, however, not as frequent.

For comparison, unpublished data from the Vosges mountains, France (48°N), were used, which were obtained during a student course, and during which similar relevée studies (species numbers, percentage of hepatics, phytomass of epiphytic bryophytes, floristic discontinuities and water storing capacity of epiphytic bryophytes) as in the Bryotrop and Bryoaustral projects were obtained.

The phytomass of epiphytic bryophytes per hectare in the Vosges mountains showed a distinct decrease from 500 kg dry weight at 600 m elev. to 150 kg at 1200 m elev., which is much less than in Chile, where up to 1700 kg/ha dry weight were calculated. One of the reasons for the differences is that the canopy is not or not as much covered with bryophytes in Europe as in the temperate and tropical rain forests. This seems to be the main distinguishing factor for true rain forests.

The percentage of hepatics in the Vosges mountains varied between 21% and 26% with peak values of 32% and 39% at 600 and 1100 m elev. This is less than along the Chile transects, where percentages of 40-80% (between 400 and 800 m at 41°S) or 30-80% (in the same elevations at 40°S) were found. All floristic parameters (calculated by a cluster analysis as well floristic discontinuities) as well as ecological parameters

resulted in an altitudinal zonation of region below 550, from 550 to 1050 m and above 1150 m.

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Literature

- Beever, J. 1999.** The south American Connection – a bryologist's view. *New Zealand Botanical Society Newsletter* 57: 10-11.
- Blüthgen, J. 1966.** *Allgemeine Klimageographie*. Berlin (de Gruyter).
- Frahm, J.-P. 1990a.** The ecology of epiphytic bryophytes at Mt. Kinabalu, Sabah (Malaysia). *Nova Hedwigia* 51: 121-132.
- Frahm, J.-P. 1990b.** The effect of light and temperature on the growth of the bryophytes of tropical rain forests. *Nova Hedwigia* 51: 151-164.
- Frahm, J.-P. 1990c.** The altitudinal zonation of bryophytes on Mt. Kinabalu. *Nova Hedwigia* 51: 133-149.
- Frahm, J.-P. 1994.** Scientific results of the BRYOTROP expedition to Zaire and Rwanda I. The ecology of epiphytic bryophytes on Mt. Kahuzi (Zaire). *Tropical Bryology* 9: 137-152.
- Frahm, J.-P., Ohlemüller, R. 2001.** Ecology of bryophytes along altitudinal and latitudinal gradients in New Zealand. *Tropical Bryology* 20: 117-137.
- Pócs, T. 1980.** The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Botanica Hungarica* 26: 143-167.
- Wardle, P., Ezcurra, C., Ramirez, C., Wagstaff, S. 2001.** Comparison of the flora and vegetation of the southern Andes and New Zealand. *New Zealand Journal of Botany* 39: 69-108.

Appendix: List of locations.

- (7) X. Region, Parque Nacional Alerce Andino ca. 45 km WSW Puerto Montt, trail to Sargazo, evergreen forest (Laurelio-Weinmannietum) 350-400 m, 41° 30' 51" S, 72° 38' 38" W, 24.2.01.
- (8) X. Region, Parque Nacional Alerce Andino ca. 45 km WSW Puerto Montt, road between park border and Rio Lenca, Laurelio-Weinmannietum, 350 m, 24.2.01.
- (9) X. Region, Parque Nacional Alerce Andino ca. 45 km WSW Puerto Montt, NE Laguna Sargazo, trail from Refugio Rio Sargazo to Alerzal, evergreen forest (Laurelio-Weinmannietum with *Nothofagus nitida*, *Saxegothaea conspicua* and *Drimys winteri*, *Fitzroyetum*, 350-500 m, 41° 30' 51,2" S, 72° 38' 38,8" W, 25.2.01 and 27.2.01.
- (10) X. Region, Parque Nacional Alerce Andino ca. 45 km WSW Puerto Montt, trail to Rodal Alerce, Laurelio-Weinmannietum and *Fitzroyetum*, 350-400 m, 27.2.01 and 22.3.01.
- (11) X. Region, Reserva Nacional de Llanquihue 50 km WSW Puerto Montt, Sector Rio Blanco, trail to volcan Calbuco, lava streams, *Fitzroyetum*, *Pilgerodendronetum*, *Nothofagus betuloides*-, *N. pumilio*- and *N. antarctica*-forest, 400-1350 m, 41° 20' 41,3" S, 72° 38' 7,4" W, 28.2.01 and 21.3.01.
- (12) X. Region, Hornopirén, Rio Blanco, alluvial forest, *Eucryphietum* with *N. dombeyi* (ca. 25 m tall), 10 m, 41° 56' 27" S, 72° 23' 26" W, 2.3.01 u. 3.3.01.
- (13) X. Region, Hornopirén, trail to volcan Hornopirén, 250 m, *Eucryphietum*, 2.3.01.
- (14) X. Region, Hornopirén, Carretera 7 between Cholgo and Pichanco, *Laurelia*-secondary forest (max. 15 m), 20 m, 42° 07' 47,3" S, 72° 27,5' 51,2" W, 3.3.01.
- (15) X. Region, Hornopirén, Carretera 7 near Cholgo, alluvial forest with predominant *Drimys winteri*, *Laurelia philippiana* and *Nothofagus nitida*, ca. 30 m, 42° 04' S, 72° 27' W., 3.3.01.
- (16) IX. Region, Parque Nacional de Huerquehue ENE Villarrica, trail to Tres Lagos, Laurelio-Weinmannietum mit *Nothofagus dombeyi*, *Saxegothaea conspicua* (to 40 m tall) on granite 750-1000 m, *Nothofagus dombeyi*-*Nothofagus pumilio*-forest 1000-1200 m, *Araucaria*-forest 1200-1250 m, 39° 08' 59,2" S, 71° 42' 52,1" W, 6.3.01.
- (17) IX. Region, Parque Nacional Villarrica, Volcan Villarrica S Pucón, road to ski area, *Nothofagus pumilio*-Forest (1300-1400 m) and *N. antarctica*-shrub at the forest line (1400-1450 m), 39° 23' 50,3" S, 71° 58' 3,9" W, 7.3.01.
- (18) IX. Region, Parque Nacional Villarrica, Volcan Villarrica S Pucón, road to Refugio Viejo, *Nothofagus dombeyi*-forest, 20 m tall, 1100 m, 7.3.01.
- (19) IX. Region, Parque Nacional Conquillio, trail from Laguna Conquillio to Sierra Nevada, *Nothofagus obliqua*-forest (1200-1250 m), *Nothofagus alpina*-*N. dombeyi*-forest (1250-1420 m), *Nothofagus pumilio*-*Araucaria araucana* (1420-forest line (1770 m)), 38° 39' 2,3" S, 71° 37' 9,5" W, 9.3.01.
- (20) X. Region, Cordillera Pelada S Valdivia, road La Union - Puiculla, Alerce-forest and bog 765-1000 m, 40° 10' 13,4" S, 73° 27' 17,2" W, 13.3.01.
- (21) X. Region, Küstenkordillere 50 km S Valdivia, Reserva Nacional Valdivia, evergreen forest with *Drimys winteri*, *Eucryphaea cordifolia*, *Laurelia philippiana*, *Nothofagus dombeyi* und *N. obliqua*, 600-650 m, 40° 02' 22,7" S, 73° 17' 54" W, 14.3.01.
- (22) X. Region, Parque Nacional Puyehue 50 km E Osorno, Sector Antillanca, Sendero El Pionero, Bosque Siempreverde, NE-slope (*Eucryphietum*), 460-675 m, 40° 44' 15,9" S, 72° 18' 53,3" W, 16.3.01.
- (23) X. Region, Parque Nacional Puyehue 50 km E Osorno, Sector Anticura, Salto del Indio, evergreen forest (*Eucryphietum* with *Nothofagus dombeyi*), 325 m, 40° 40' 7,3" S, 72° 10' 20,1" W, 16.3.01.
- (24) X. Region, Parque Nacional Puyehue 50 km E Osorno, Sector Anticura, trail to Mirador El Puma, *Eucryphietum* 350-650 m, 16.3.01.
- (25) X. Region, Parque Nacional Puyehue 50 km E Osorno, Sector Antillanca, Laguna El Espejo, *Eucryphietum* with *Nothofagus dombeyi* and *Saxegothaea conspicua*, 500 m, 18.3.01.
- (26) X. Region, Parque Nacional Puyehue 50 km E Osorno, Sector Antillanca, Rio Pescadero, *Saxegothaea conspicua*-*Nothofagus dombeyi*-forest ca. 30 m tall, 700 m, 18.3.01.
- (27) X. Region, Parque Nacional Puyehue 50 km

E Osorno, Sector Antillanca, above Lago El Toro, *Nothofagus dombeyi*-Forest with *Laurelia philippiana* (bis 30 m tall) and dense *Chusquea* understorey, 750 m, 18.3.01.

(28) X. Region, Parque Nacional Puyehue 50 km E Osorno, Sector Antillanca, *Nothofagus dombeyi*-*Saxegothea conspicua*-forest with *Chusquea*- understorey, 850 m, 18.3.01.

(29) X. Region, Parque Nacional Puyehue 50 km E Osorno, Sector Antillanca, *Nothofagus dombeyi*-*N. betuloides*-forest (ca. 20 m tall) on lava, 950 m, 18.3.01.

(30) X. Region, Parque Nacional Puyehue 50 km E Osorno, Sector Antillanca, near Centro de Ski, *Nothofagus pumilio* forest (max. 15 m) 1050-

1160 m, *Nothofagus pumilio*-*N. antarctica*-forest 1160 m – forest line (1200m), 18.3.01.

(31) X. Region, Road Hotel Termales – Argentinian border at Parque Nacional Puyehue, 50 km E Osorno, Myrtaceen- swamp forest in the valley of Rio Gol Gol, 200 m, 40° 40' 27,4'' S, 70° 17' 23,3'' W, 19.3.01.

(32) X. region, Parque Nacional Puyehue 50 km E of Osorno, Sector Anticura., Salto del Indio, evergreen forest (“*Eucryphietum*” with *Nothofagus dombeyi*), 325 m alt., 19.3.01.

(33) X. Region, Vicente Perez Rosales National Park, road to Refugio Vulcan Osorno, *Eucryphietum* with *Nothofagus dombeyi*, 400 m, 20.3.01.

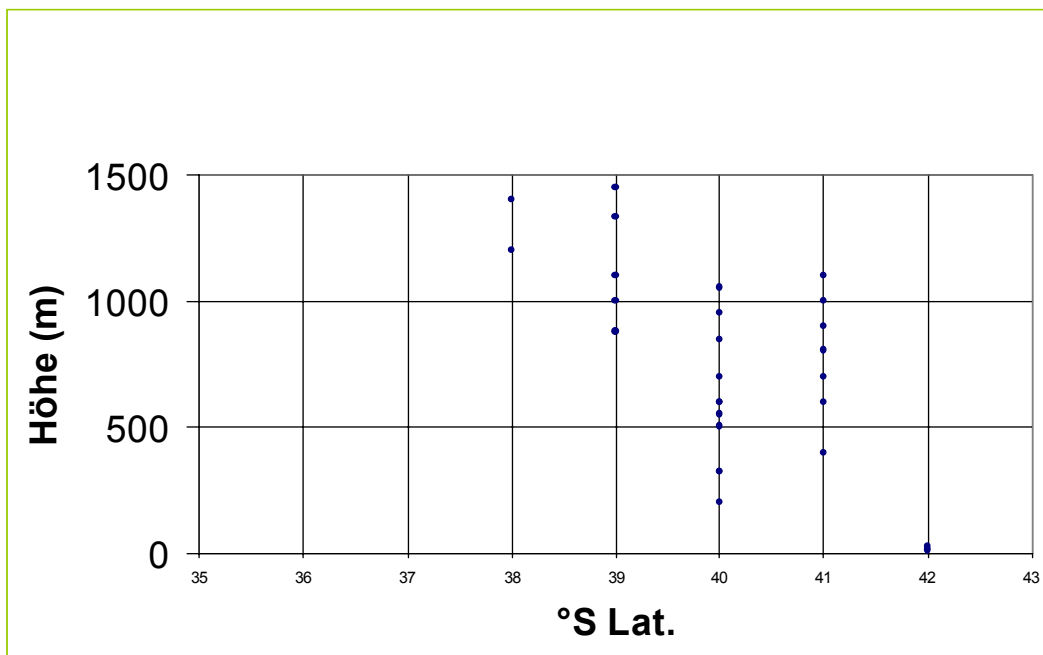


Fig. 1: Location of the transects studied in Chile within the Bryoaustral project.

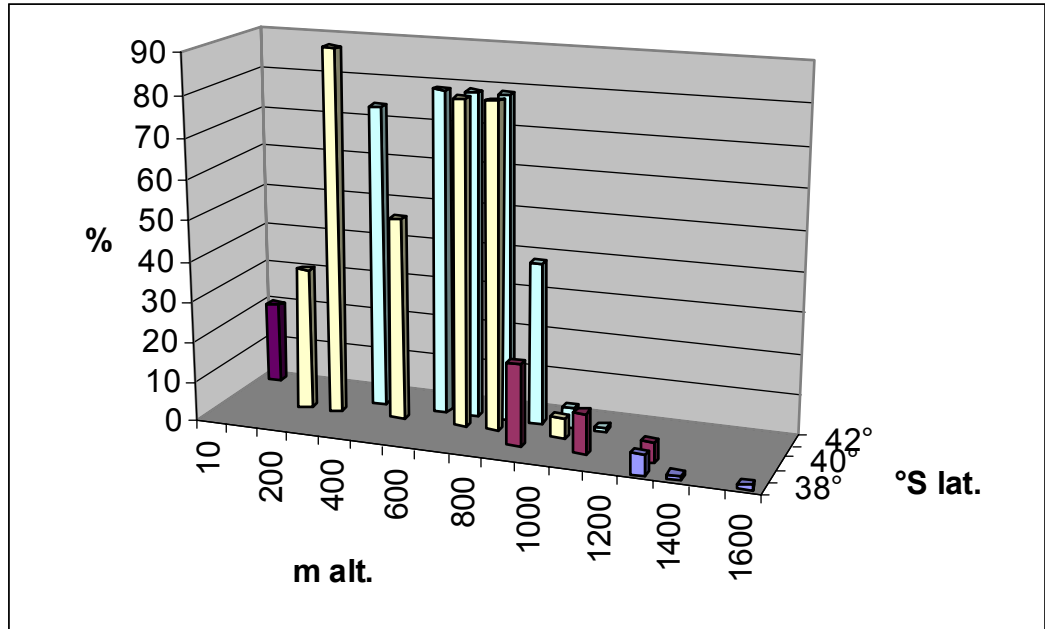


Fig. 2: Percentage cover of epiphytic bryophytes along latitudinal and altitudinal gradients in S-Chile.

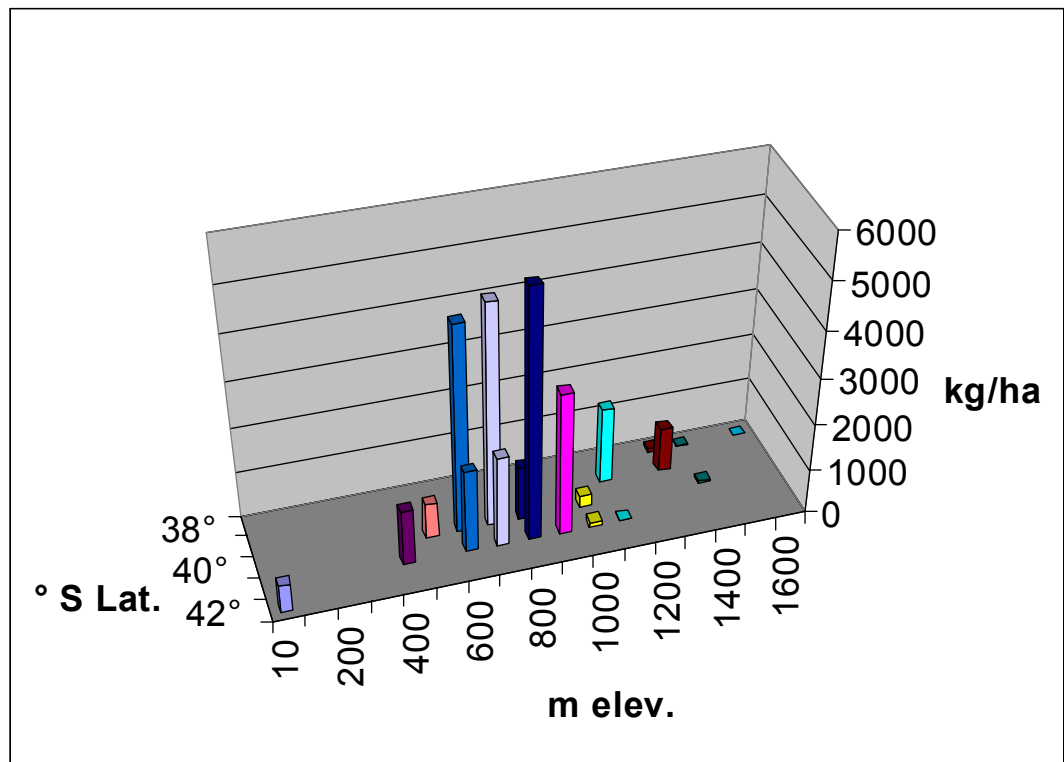


Fig. 3: Phytomass of epiphytic bryophytes in kg/ha wet weight at different latitudes and altitudes in Chile.

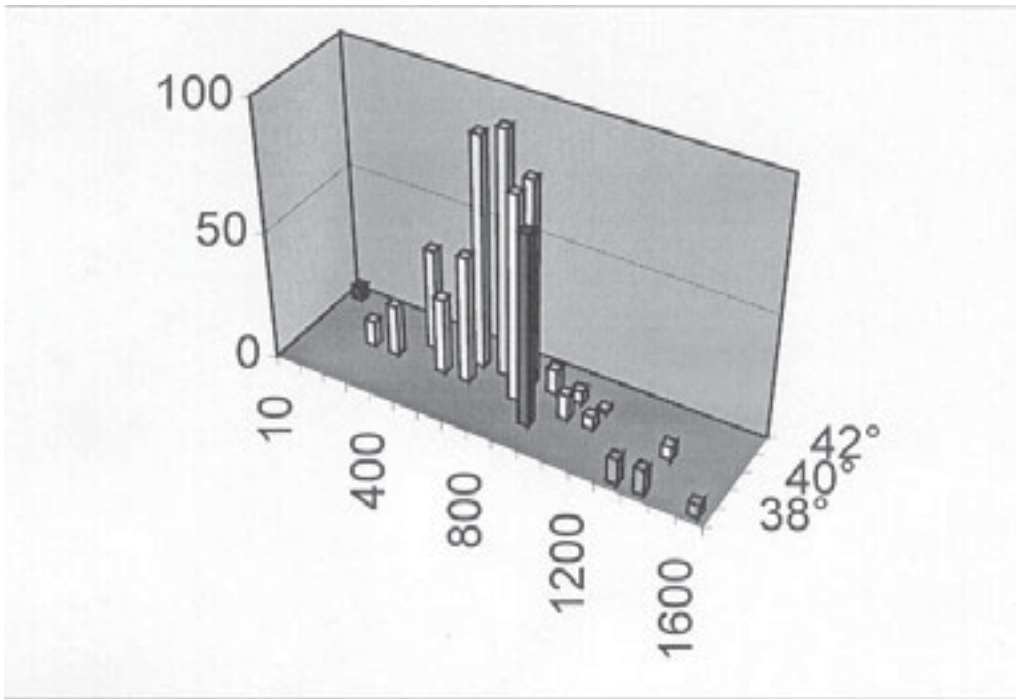


Fig. 4: Percentage of hepatics in the relevés.

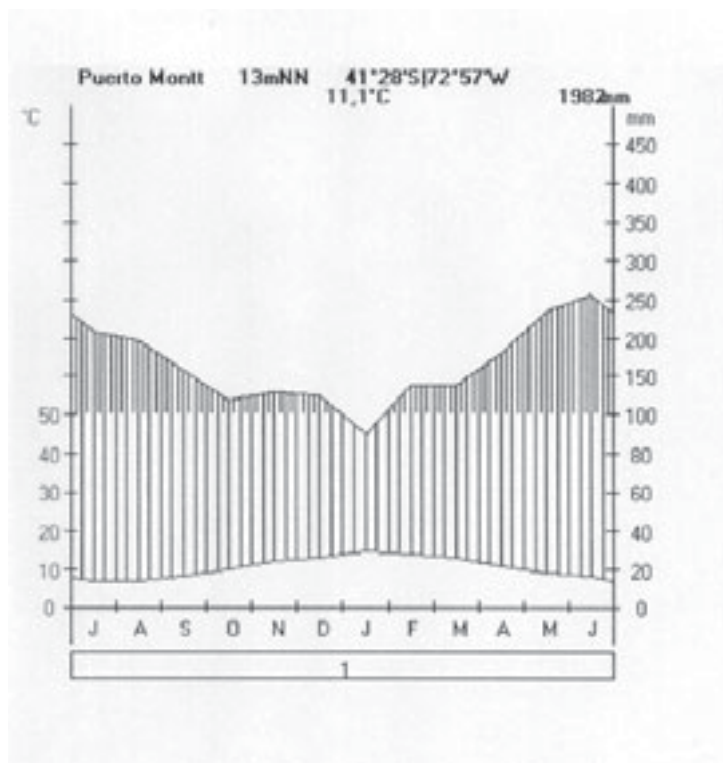


Fig. 5: Climate diagram of Puerto Montt, showing a distinct “dry season” during summer.

