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Ecology of bryophytes along altitudinal and latitudinal gradients in New Zealand. Studies in austral temperate rain forest bryophytes 15.

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Abstract: Six altitudinal transects through temperate rain forests were studied at different latitudes in the South and North Island of New Zealand with respect to species numbers of bryophytes, cover and phytomass of epiphytic bryophytes, composition of life forms and ratio liverworts : mosses. Phytodiversity of bryophytes is almost constant from the lowlands to the high montane belt but decreases in the subalpine belt. Similarly, phytomass and cover increase with elevation but decrease in the subalpine belt. The percentage of liverworts increases accordingly and can reach maxima of 80-90%. The most significant life forms are tails and wefts characteristic for hyperhygric conditions, pendents for cloud belts and cushions for subalpine belts. The altitudinal gradient is much stronger then the latitudinal gradient, that means the differences between the elevations within a transect are more important than the differences between the transects. They are attributed to the humidity.
The temperate rain forests of New Zealand have similar bryological characteristics as the tropical rain forests in equatorial latitudes in 2000 – 3000 m altitude but differ in the drier subalpine belt and higher phytomass.

1. Introduction

Large parts of New Zealand are characterized by an abundance of bryophytes, especially in the moist western side of the Southern Alps on the South Islands and at the mountains of the North Islands. The mass of bryophytes, which covers not only the forest floor but also trunks and branches provides the typical rain forest aspect. Few attempts were made so far to study the bryophytes as the most characteristic part of the rain forests. First studies were undertaken within the German BRYOTROP project in different part of the tropics (South America, Africa, SE-Asia, cf. Frahm 1987, 1990, 1994c), where transect studies from the lowland forest to the forest line were performed to get a first impression of the floristic composition on hectare plots, the changes of phytodiversity along the altitudinal gradient, the phytomass, ecological conditions, life strategies, morphological adaptations and phytosociology of epiphyte communities. The BRYOAUSTRAL project was established amongst others to collect similar data of the temperate rainforests of the southern hemisphere. New Zealand provides the best conditions for such study. It has still large undisturbed forest areas and for the transect studies, the forest line is reached all along the south Island and in some parts of the North Islands. Due to a N-S extension of about 1500 km, New Zealand offers in addition the interesting chance to determine the species diversity and other parameters not only along altitudinal gradients from the lowland to the forest line but also along a longitudinal gradient over a long distance from North to South and a W-E gradient, which is characterized by the amount of precipitation. By this way, the bryophyte diversity can be determined within a threedimensional model.

The studies should help to find answers for following questions:

A. Evaluations within a single transect:
1. how is the species richness expressed by species numbers all of the hectare plots studied?
2. how is the biodiversity distributed along the transect? Is there a gradient along the transect and if, is there an increase or a decrease from low to high elevations?
3. How is the altitudinal zonation of the forests along the transect based on bryophytes?

B. Comparison of different transects.
1. How are the different transects related to each other with regard to their species composition, species richness, cover, ratio liverwort : mosses etc. ?
2. Are the differences within one transect (along the altitudinal gradient) greater than between different transects at different latitudes? Is elevation or latitude the determining factor ?

C. Comparison with tropical rain forests.
1. Are the parameters observed in the temperate rain forests of New Zealand (species number per relevée, altitudinal gradients, life forms, moss-liverwort index etc.) comparable with tropical rain forests or are there differences between tropical and temperate rain forests with regard to the bryophyte vegetation ?
2. Have tropical and temperate rain forests parameters in common with regard to their bryophyte vegetation which allows to define the term rain forest bryologically ?
3. Which latitudes in the tropics resemble the temperate rainforests in New Zealand with regard to their „mossiness“ (cover) or species richness ?

A similar study of the same transects and study areas but based on higher plants was published by Ohlemüller & Wilson (2000).

2. Methods

2.1 Study areas

Field work was carried out in February and March 1998. During fieldwork, 34 hectare plots were studied in forests in 200 m altitudinal intervalls along 6 transects from the lowland, many to the forest line. The S-N distance between the transects is approx. 5° = 555 km.
The hectare plots were chosen in homogoneous forest sites, which gives a good base for comparability.

The location of the transects is given in fig. 1, that of the plots in tab. 1.

South Island
Transect 1 (Plots 1-7): Haast Pass Highway (incl. Lake Ellery, Jackson Bay Road), lowland - subalpine (20 - 800 m a.s.l.), 43°56´S - 44°07´S , 169°10´W - 169°25´W, mixed podocarp broadleaved beech forest / beech forest / beech broadleaved forest. Precipitation 3455 mm/year.
Transect 2 (Plots 8-14): Franz Josef Glacier area: Alex Knob Track at Franz Josef Glacier, Morraine Walks at Fox Glacier, Bruce Bay Road, Gillespie Beach Road, lowland - subalpine (30 - 800 m a.s.l.), 43°24´S - 43°25´S, 170°09´W - 170°10´W, podocarp broadleaved forest / broadleaved forest. Precipitation 5920 mm/year.

Transect 3 (Plots 15-20): St. Arnaud area: Range and Sloop Track, Mt. Robert, lowland - sub alpine (630 - 1400 m a.s.l.), 41°49´S , 172°52´W, beech broadleaved forest / beech forest. Precipitation 1575 mm/ year.

Transect 4 (Plots 21-27): Karamea area: Mt. Stormy Track, Oparara - River and Kohaihai - River, lowland - montane (20 - 1000 m a.s.l.), 41°06°S - 41°12´S 172°08´W - 172°12´W, broadleaved forest / mixed podocarp broadleaved beech forest. Precipitation 2410 mm/ year.

North Island

Transect 5 (Plots 28-32): Ohakune Mt. Road on Mt. Ruapehu, (incl. Rangataua Road), lowland - subalpine (650 - 1450 m a.s.l.), 39°19´S - 39°24´S, 175°25´W, podocarp broadleaved forest / mixed podocarp broadleaved beech forest / beech forest. Precipitation 2845 mm/ year.

Transect 6 (Plots 33-38): Urewera National Park area: Lake Waikareiti track and Manuoha Hut track, lowland - montane (600 - 1150 m a.s.l.), 38°40´S - 44°30´S, 177°05´W - 177°09´W, beech forest. Precipitation 2050 mm/year.

2.2. Methods

In every hectare plot the following parameter were determined:

a. The number of bryophyte species (species richness, α-diversity, occurrence). Since all study areas are of the same size, these data can also be used by determining the frequency of species in the different plots along the transect. The common species were noted in the field, other species were collected and determined after fieldwork. Specimens are deposited in the herbarium of the author (BONN), duplicates in the herbarium of Landcare Research Christchurch (CHR).

b. The cover of bryophytes on soil, rock and rotten wood as well as on trees.

c. The ratio of the quantity of liverworts and mosses.

d. Percentage of life forms using the a modified classification by Mägdefrau (1982): turfs, dendroids, tails, pendants turfs, wefts, mats and cushions. This list excludes annuals (which is a life strategy), makes no difference between short and tall turfs as well as tails and fans and includes dendroids (which is a growth form) in the sense of dendroid turfs. A major point is that not too much different life forms should be differrentiated because too much categories hide the trends. The life form categories were previously much based on their different morphology but should express ecological adaptations and should also be redefined ecophysiologically. Therefore different life forms can be significant for the same adaptation. The exact application of life forms is not always unproblematical and requires explanation:

Dendroids include here true dendroid species such as *Dendroligotrichum dendroides* as well umbrella mosses (*Hypopterygium* spp., *Hypnodendron* spp.), and dendroid liverworts (*Plagiochila* spp.) or umbrella liverworts (*Hymenophyton* spp., *Symphyogyna* sp.).

Tails include typical mosses such as *Cyathophorum bulbosum*, but also Hookeriaceae, species of *Plagiochila* and species of *Schistochila, Lopidium concinnum, Echinodium*, *Cyrtomnion, Cyrtopus, Hymenodon, Calomnion* and species of *Symphyogyna*. Fans are included in tails. The differentiation concerns only a growth form (branched vs. unbranched), which makes no difference with regard to the water uptake and the fact that both have no contact with other plants and are not attached to the substrate. Species with creeping stems and erect branches (*Mesotus, Macromitrium, Dicnemon*) are also included here, although they are confined to higher altitudes and are adapted to dry conditions.

Pendants usually consist of *Weymouthia cochleariifolia, W. mollis* and *Papillaria* spp. This life form is a modification as shown by the fact that these species are found creeping and not pendant in drier conditions. In contrast, species of *Lepidolaena, Porella, Mesotus, Dicnemon* and *Wijkia* are found in pendant forms in humid habitats

Turfs include species of *Dicranoloma, Ditrichum, Rhizogonium*, but also *Ptychomnion aciculare* and certain species of *Plagiochila.*
Wefts are represented by *Lepidozia* spp. and *Trichocolea* spp. The inclusion of *Thuidium* as proposed by Mägdefrau must be doubted, because it characterizes much drier habitats as those of *Lepidozia* or *Trichocolea*.
Mats are attributed to *Hypnum* spp., *Wijkia* sp. and other pleurocarps but also thallose hepatics (*Monoclea, Aneura*). Perennial thalli such as *Monoclea* were not considered by Mägdefrau. (thallus is a growth form).
Cushions are typically formed by *Leptostomum* in the subalpine.
In several cases an exact application of a life form was difficult, e.g. in species of *Riccardia* growing upright, species of *Bazzania* somewhat intermediate between mats and turfs. In addition, turfs and cushions are not always clearly be separated. Stands of *Dicranoloma* can be almost cushion-like in drier habitats but form loose turfs in wetter habitats. This concerns also the classification of "mossballs" consisting of species of *Dicranoloma, Herbertus* and *Chandonanthus*.
Due to the insufficient knowledge, phytogeographical evaluations could not be performed. Observations of sterility or asexual viz. sexual propagation were begun but not continued since they seemed not to give sufficient results.

e. The phytomass of epiphytic bryophytes (wet weight) on 0.5 m^2. For the determination, the epiphytic bryophytes were scraped off the bark of a representative tree trunk in each plot in 1-2 m height. The material was soaked in water for 12 hrs and weight with a balance after the excess water was shaked off. The dry weight could not be determined in the field because there was no chance to get the bryophytes dried. However, according to our experience in various parts of the tropics, the wet weight is generally 3 times higher than the dry weight (Frahm1990, 1994c).
g. Microclimatic measurements of temperature and air humidity were made over a period of 3-5 days in different altitudes of the transect using Tinytalk (Orion Co.) dataloggers.

3. Results

3.1 Phytomass

The "mossiness" of a rain forest is well expressed by the amount of phytomass produced by bryophytes. It was characterized by the weight of the bryophyte layer on 0.5 m^2 of a tree trunk in every relevée. The phytomass depends on the humidity of a habitat (precipitation = nutrient supply and length of periods >80% rH during daylight = length of photosynthetic period), and since the precipitation differs in the transects studied between 1600 and 6000 mm, it cannot directly be compared. Generally an increase of the phytomass with elevation can be observed, which corresponds with increasing precipitation and cloud layers (fig. 2). Thus the phytomass increases along the Haast transect from 630 g/ 0.5 m^2 near sea level to 2800 g/0.5 m^2 in 600 m elevation. Although the precipitation (based on the values of the climate station, which can differ from the relations in the field) is "only" 3450 mm/year but almost 6000 mm/year in the Franz Josef Glacier area, the phytomass along the latter transect is not higher but increases from 250 g/ 0.5m^2 at 200 m elevation to 800 g/0.5m^2 at 800 m, being considerably higher in two swamp forests shortly above sea level, where 540 and 580 g were measured. Maximum values are reached at 800 m in the South Island and 1000 – 1200 m in the North Island. This is in accordance with a change in the forest structure from high montane to subalpine forests. Although the subalpine forests are much lighter, which could favour epiphyte growth, they are apparently much drier, which is expressed in a drastic change of epiphytic bryophyte communities and the life forms of their species (Lindlar & Frahm in press). The determination of phytomass per 0.5m^2 is therefore also an expression of the different life forms composing the bryophyte layer on tree trunks. It cannot be used as parameter for the epiphytic bryophyte production of an altitudinal belt, because of the uneven distribution of bryophytes on different trunks and on trunks and canopy.
Phytomass production is, however, controlled by a combination of light, temperature, water and nutrient supply and not correlated with a single parameter. Thus there was no correlation for

example between the phytomass and the relative light intensity measured

3.2 Cover of epiphytic bryophytes

The values for the percentage cover of bryophytes on soil and especially on bark are relatively characteristic for the altitudinal belts, which is shown by values derived from different relevées at the same altitude. Deviations are only possible e.g. on mountain ridges, which are not comparable with slopes, in the case that woods were burnt or host trees infected by fungi. Cover of bryophytes on the forest floor was estimated but not evaluated because it varies much and seems to depend much on the competition of flowering plants and ferns, different from tropical forests, where this effect cannot be observed

The cover of epiphytic bryophytes along the transects is shown in fig. 3. It is not correlated with the precipitation. Transects with higher precipitation such as Mt. Ruapehu, North Island have 35-40% cover between 600 and 1400 m whereas transects with lower precipitation such as St. Arnaud, South Island, have higher values, an indication that bryophyte cover of epiphytes is not determined by precipitation but humidity (fog, cloud cover). Generally there is an increase of the cover of epiphytic bryophytes with the altitude. Maximum values are reached at elevations with frequent cloud layers or situations (depressions, lake shores) with frequent mist in the morning, an effect, which can also be observed in other parts of the world similar to the elfin forests in the tropics. In the subalpine belt as in the St. Arnaud transect at 1400 m, there is a sudden decrease of cover values combined with a change of life forms with water storing adaptations as an indication of strong evaporation. Along the Franz-Josef and Karamea transect, high cover values are found already shortly above sea level, which are higher than those from the next slopes, which is interpreted by the higher humidity in these stands either by swamp forests or by frequent fog in the coastal plains.

The cover values are not directly correlated with the phytomass, because large covers of thin crusts give only small phytomass values.

3.3 Ratio liverworts : mosses

The estimation of the ratio between liverworts and mosses is an easy tool to determine the relative humidity of a stand and to compare different relevées in this respect. It is based on the experience that liverworts increase with increasing humidity, either on a continental scale, a regional scale or along a transect. In Europe, there is a distinct increase of liverworts from E to W (Düll1984). In the Chocó region, one of the regions in the world with the highest precipitation of 15 m/year, liverworts count for 80% of the bryophytes (Frahm 1994a). Liverworts also increase with the altitude in the tropical rain forests (Frahm 1994b). Reason is the lower drought tolerance of liverworts.

Liverworts generally show a distinct increase along the altitudinal transects (fig. 4), from 35 viz. 40% to 80% along the Haast and Franz-Josef transects and from 50% to 90% in the Karamea transect. This correlates with high precipitation (Haast: 3455 mm/year, Franz-Josef 5920 mm/year) They are distinctly less represented in transects with lower precipitation as in the drier St. Arnaud transect (1545 mm/year), where liverworts do not exceed 10%.

3.4 Species diversity

Species numbers do not vary much along the transects (fig. 5). They range between 30 and 50 at elevations up to 1000 m. Above 1000 m there is a sudden decrease of diversity which correlates with lower cover values as well as phytomass values and indicates a major climatic change.

3.5 Life forms

The composition of life forms characterizes much the appearance of the bryophyte vegetation. A life form spectrum allows to obtain a realistic impression of the habitat (e.g. a lowland forest with 40% pendants on branches, 30% dendroids in the forest floor in contrast to a subalpine forest with 60% cushions). Life forms reflect furthermore much the different ecological conditions of a region (different altitudinal belt, different latitudes), they are a response of the vegetation to the ecological parameters. Life

forms are mostly correlated with the humidity factor (water uptake, water retention).
The transects are characterized as follows:

1. Haast Pass (fig. 6b)
As in the previous transect, dendroids (umbrella shaped *Hypnodendron* spp. and *Hypopterygium* spp.) are most characteristic for low altitudes. They disappear above 400 m. Cushions are confined to high altitudes (600 – 800 m). Wefts have a maximum at 600 m, where *Lepidozia pendulina* is dominant on the forest floor as well as lower tree trunks. Pendants are less frequent as in the Franz-Josef Glacier transect, perhaps because of the less frequent mist.

2. Franz-Josef Glacier (fig. 6a)
Dendroids is the predominant and highly characteristic life form in the lowlands. They consist of species of *Hypnodendron* and *Hypopterygium*. The percentage is gradually reduced to 400 m alt. The dendroids at 800 m, however, consist of *Dendroligotrichum dendroides*. In contrast, pendants are represented at lower altitudes with only small percentages and reach their maximum at 600 m but disappear almost totally at 800 m. They are significant for cloud forests. Turfs lack in the coastal lowland forest but increase slightly with altitude and reach their maximum at 800 m. Wefts, mats and tails are represented at all altitudes with low and varying percentages but no distinct trends.

3. St. Arnaud transect (fig. 6d)
The driest transect of all transects studied is characterized by a high percentage of turfs (mainly of*Dicranoloma* spp.), even considerable amounts of cushions through the transect reaching a maximum in the subalpine forest at 1400 m, almost lack of pendants, almost constant presence of mats through the transect as well as tails until 1000 m. The distribution of dendroids (here only *Dendroligotrichum*) is inconstant because determined by chance. This species forms large clones and can reach high cover values as here at 1200 m. It is also to be considered that this transect starts at 600 m and not at sea level as the previous ones, which is expressed in the lack of pendants (except for 800 m, a cloud layer), low values for tails and wefts and lack of umbrella bryophytes.

4. Karamea (fig. 6c)
Also here the dendroids are well represented in the lowlands by umbrella mosses, vanishing at medium altitudes and being replaced by *Dendroligotrichum* at higher altitudes. Similar to the previous transects, pendants have also their maximum at lower altitudes but disappear above 600 m. Wefts increase with altitude with a maximum at 800 and 1000 m and cushions are found only in the subalpine (1000 m).

5. Ruapehu transect (fig. 6e)
The Mt. Ruapehu transect starts also at 600 m and is – like the St. Arnaud transect - no more situated along the coast, although has a higher precipitation as transect 4. Both is expressed by the higher percentage of cushions, especially above 1000 m, decrease of wefts with increasing altitude, decreasing tails (only up to 1000 m) and increasing mats.

6. Urewera transect (fig. 6f)
This transect starts also at 600 m like both previous transects but is more humid. This is expressed a smaller percentage of cushions and a higher percentage of turfs. The higher altitudes are moister as in the Ruapehu transect, as expressed by increasing percentages of wefts and higher percentages of pendants (although not as high as in the coastal transects 1-3 along the South Island).

In conclusion, tails, wefts, dendroids, pendants and cushions have proved to be the most significant life forms along the studied transects. Tails, wefts and possibly also dendroids seem to indicate surplus water supply. These life forms have no mechanisms for water retention, in opposite, they have a maximal surface and thus a maximal evaporation, which is only possible in hyperhygric conditions. Pendants have local significance for altitudes with frequent clouds or mist. In contrast, cushions indicate the drier conditions.

3.6 Microclimatic measurements

Microclimatic measurements especially of the relative humidity can give a good illustration of the habitat conditions of bryophytes. Although only periods of 2-4 days were measured, the data show characteristics of the habitats, which give good explanations for the life form spectra in the different transects and elevations.

Along the **Haast transect**, the humidity was so high that the humidity dataloggers did not properly work. The range of temperatures was similarly low along the Haast transect and was 10–14°C at 50 m alt. (fig. 7d) but 8-12°C at 400 m during the same period, showing a low decrease with altitude due to the high humidity. The difference between day and night was 4°C on two sunny days but only 1°C on a rainy day.

Measurements were taken along the **Franz-Josef Glacier transect** in 200 m and 400 m. At 200 m, the humidity went not below 90% even at noon at a more open microhabitat (fig. 7a) and reached almost consistently the dew point in a less open habitat as well as in 400 m (fig. 7b). Thus the bryophytes are consistently wetted and have consistently photosynthesis over the light period. The habitats are also characterized by high nutrient input by high precipitation (around 6000 mm/year), which results in high phytomass production. Permanent humidity and high rainfall has, however, physiological problems with regard to gas exchange. Bryophytes attached to the ground or growing in mats can be covered by water which reduces much the gas exchange. Therefore the prevailing life forms are umbrella mosses, wefts and tails providing a maximum of surface.

The temperatures varied during the same period between 8°C in the early morning hours and 14°C at noon but 11° C and 14°C at 400 m (fig. 7c). (Temperature measurements were taken in the same spots as the humidity measurements). It shows considerably low day/night differences of 6°C viz. 3°C typically for oceanic climates.

All humidity dataloggers along the **St. Arnaud transect** at 600, 800 and 1000m showed also a breakdown during the same period but all registered humidities between 90 and 100% during the other periods. The temperatures varied between 14 and 16°C at all elevations during cloudy days and reached 22° during a sunny day (fig. 7g). The temperatures in the inland are thus higher even at higher altitudes as along the coast.

Also along the **Karamea transect**, the humidity was most parts of days and nights above 90% during a period of five days and equally in 200, 400 and 600 m alt. (fig. 7e), interrupted only by short periods at noon, when the humidity dropped to 50% for only a short while. Reason were sudden increases of temperature to almost 20°C or more (fig. 7f) during sunny seasons. The highest values of rH were measured at 200 m alt. The temperature dropped not down below 10° due to the more northern location of the transect as compared to the previous transects.

The daily temperatures along the **Ruapehu transect** in 650, 100 and 1450 m varied much more due to the location in the interior of the North Island, between 8°C and 2°C in clear nights and 13°C and 15°C in cloudy nights, 16°C and 20°C during sunny days and 6°C and 10°C during cloudy days, thus more "continental" relations as compared with the transects along the west coast of the South Island.

Similar ranges were found along the **Urewera transect**, where the temperatures in 600m and 1000 m varied between 7°C and 15°C at day and night but reached 22°C on a sunny day (fig. 7h). Conspicuously the temperatures, although taken in 400 m altitudinal difference, showed only few differences, which illustrates that the microclimate can compensate much differences in altitude

4. Discussion

Although obtained with relatively simple methods, this study allows the outline bryological characteristics of the temperate rainforests of New Zealand, the variation along altitudinal and latitudinal gradients and also a comparison with tropical rain forest in different parts of the world studied during the BRYOTROP projects.

Common bryological characteristics of the temperate rainforests of New Zealand are:

1. High phytomass values of epiphytic

bryophytes with maximum values of 5.6 kg/m^2.
2. An increase of bryopyhte phytomass from the lowland to the high montane belt but a decrease in the subalpine belt.
3. High epiphyte cover values.
4. High percentage of liverworts
5. High species numbers per area with a decrease in the subalpine.
6. Tails, dendroids, wefts as characteristic life forms from the lowland to the submontane belt, pendants characteristic in foggy or cloudy areas and cushions in the subalpine belt.

Humidity seems to be the most important factor for bryophytes: it determines phytomass, cover and percentage of liverworts. These parameters are generally lower along the transects with lower rain fall. The altitude has also effects on these factors, but seems to be correlated with the humidity (increasing rain fall, cloud cover and mist frequency) with elevation. Latitude (a difference of 5°) has only small influence on the bryophyte vegetation; it raises the forest line about 400 m and causes a drier climate because of higher temperatures and higher evaporation. Therefore the different relations along the transect on the North Islands are more attributed to the humidity than to the latitude. Species richness is not effected by latitude or altitude but generally only lower in the subalpine belt. The species richness of higher plants was also determined much more by altitude than by latitude (Ohlemüller & Wilson 2000).
Our results are in accordance with those of Vitt (1991), who studied a transect over 40° in the same region from Campbell Island S of mainland New Zealand to Vanuatu in Oceania. He found that species richness is constant over the latitudes, however, increasing with elevation, which could not be confirmed in New Zealand, perhaps because Vitt´s study was based only on mosses.

A comparison with studies from tropical rain forests (Frahm 1987, 1990, 1994c) shows that only altitudes above about 2000 m in the tropics can be compared with temperate rain forests in New Zealand (fif. 8). This is presumably due to the different climatic conditions in the tropical lowland and (sub)montane regions. Although the precipitation may be comparable, the temperatures are much higher in the tropics, causing physiological problems for the bryophytes. The rain forest in 0-1000m in the temperate regions is thus comparable to the montane to subalpine forest in the tropics. This is confirmed by the fact that several species (*Lepyrodon tomentosus, Monoclea gottschei*) found in the temperate rain forests in southern Chile have migrated north into the Andes and are found again in Colombia and Venezuela 2000 m higher, according to the relative habitat consistency of species. Other temperate rain forest species such as *Dicranoloma billardieri* are found again in the mountains of Central Africa. This is also confirmed by the fact that many genera typical for temperate rain forests are found in tropical rain forests at altitudes above 2000 m such as liverwort species of *Lepicolea, Chandonanthus, Herbertus, Bazzania, Plagiochila* or *Lepidozia*.
Above 2000 m we have similar climatic conditions as well as bryophyte vegetation in both rain forests types. This includes similar life form spectra, phytomass and cover. Thus the montane forest of the tropical rainforest in equatorial latitudes can be compared with the lowland rain forest in 40°S, the high montane tropical with the montane temperate and the subalpine tropical with the high montane temperate forest (fig. 8). This becomes not so evident from the climatological data: the mean annual temperatures in New Zealand vary between 8° and 11°C at the base of the transects. This corresponds to 2900 – 3300 m alt. at Mt. Kahuzi in Zaire (Frahm 1994a), however, the temperature in New Zealand is much depressed because of the oceanic influence and not directly comparable with the situation in the midth of the African continent.

There is, however, a distinct differences between the both rain forest types:
Whereas the values for cover and phytomass in tropical rain forests increase towards the forest line, there is a decrease in the temperate rain forests of New Zealand in the subalpine belt. This effect is attributed to the drought at this elevation, which is expressed by drought tolerant life forms. It corresponds with the scheme in fig. 8, in which the subalpine temperate forest is comparable with

the regions in the tropics above the forest line.

The phytomass of epiphytic bryophytes determined in Central Africa (Frahm 1994c, here calculated for wet weight) was 60 g/m^2 at 900 m alt., 210 g/m^2 at 1900 m, 300 g/m^2 at 2900 and 1800 g at 3300 m and thus distinctly lower than in all transects in New Zealand. Maximum values in Borneo (Frahm 1990) were 1360 g/m^2 wet weight at 3300 m alt. and thus comparable to St. Arnaud 800 m or Haast 1300 m.

The bryological parameters indicate the following altitudinal zonation of the temperate rain forests in New Zealand:

1. A lowland zone > 200 m which is weakly distinguished by lower phytomass and cover (not in swamp forests in the Franz-Josef glacier transect), lower percentage of liverworts (not in the Karamea transect) and composition of life forms.
2. The montane zone from 200 to 800 – 1400 m, which can hardly be differentiated in any sub- or high montane zone. The varying upper limit depends on the latitude and humidity. It is lowest in the southernmost transect in the South Island and raises with increasing latitude and decreasing precipitation.
3. The subalpine zone above 800 – 1400 m characterized by dramatical reduced values for cover, phytomass, species numbers, liverwort percentage and change of the composition of life forms.

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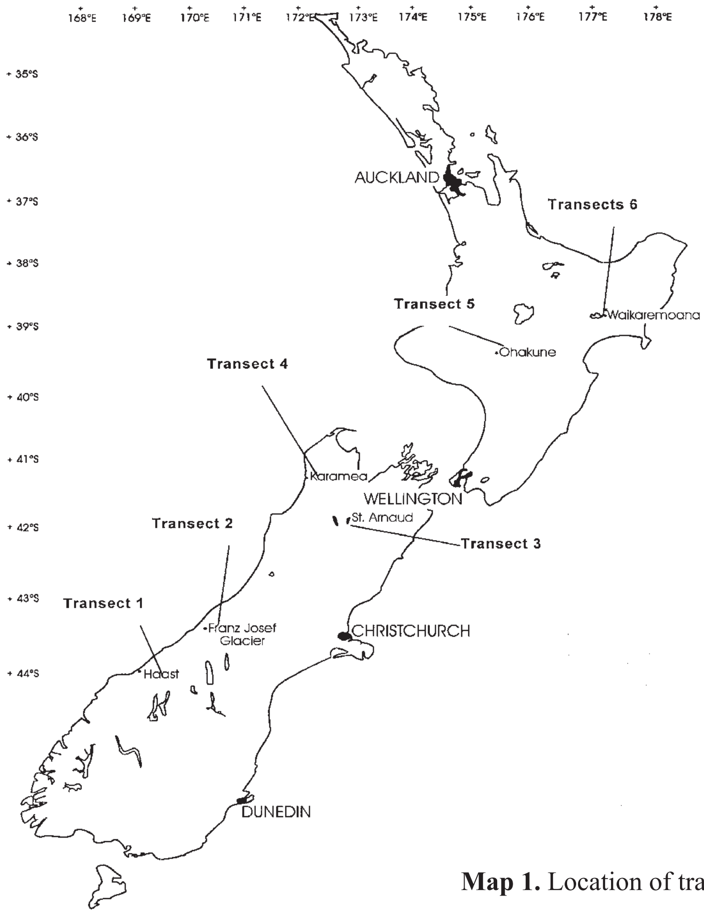
Tab. 1: Location of the study areas

Plot	Date	Lat. [S]	Long. [E]	Transect	Altitude
1	26.02.1998	44° 04'	168° 40'	1	20
2	26.02.1998	44° 01'	168° 46'	1	20
3	22.02.1998	43° 58'	169° 10'	1	40
4	25.02.1998	44° 03'	169° 22'	1	200
5	25.02.1998	44° 02'	169° 25'	1	400
6	21.02.1998	44° 07'	169° 21'	1	590
7	24.02.1998	44° 07'	169° 21'	1	800
8	20.02.1998	43° 40'	169° 35'	2	30
9	19.02.1998	43° 25'	169° 51'	2	50
11	15.02.1998	43° 25'	170° 10'	2	190
12	18.02.1998	43° 24'	170° 10'	2	420
13	18.02.1998	43° 24'	170° 10'	2	600
14	16.02.1998	43° 24'	170° 09'	2	800
15	08.03.1998	41° 48'	172° 51'	3	630
16	08.03.1998	41° 49'	172° 52'	3	800
17	07.03.1998	41° 49'	172° 48'	3	850
18	06.03.1998	41° 49'	172° 52'	3	1000
19	06.03.1998	41° 49'	172° 52'	3	1250
20	06.03.1998	41° 49'	172° 52'	3	1400
21	03.03.1998	41° 07'	172° 06'	4	20
22	02.03.1998	41° 10'	172° 10'	4	200
23	02.03.1998	41° 10'	172° 10'	4	200
24	04.03.1998	41° 17'	172° 13'	4	350
25	04.03.1998	41° 17'	172° 13'	4	600
26	01.03.1998	41° 17'	172° 13'	4	800
27	01.03.1998	41° 17'	172° 13'	4	1000
28	15.03.1998	39° 24'	175° 25'	5	650
29	16.03.1998	39° 23'	175° 27'	5	800
30	14.03.1998	39° 21'	175° 29'	5	1020
31	14.03.1998	39° 20'	175° 30'	5	1220
32	14.03.1998	39° 19'	175° 31'	5	1450
33	21.03.1998	38° 45'	177° 10'	6	600
34	21.03.1998	38° 44'	177° 11'	6	800
35	19.03.1998	38° 44'	177° 10'	6	950
36	22.03.1998	38° 41'	177° 7'	6	680
37	22.03.1998	38° 41'	177° 7'	6	1000
38	20.03.1998	38° 41'	177° 7'	6	1150

Table 2. Studied transects.
Precipitation and temperature was determined from climatological datasets (obtained from Climate Research and Information Services, Wellington, NZ) of the nearest available station. Values given here are therefore only approximate.

No.	Transect	Altitudinal range [m a.s.l.]	Precipitation [mm/year]	Temperature [mean annual ºC]
1	**Haast Pass**	20 - 800	3455	< 8
2	**Franz Josef Glacier**	30 - 800	5920	9
3	**St. Arnaud**	630 - 1400	1575	9
4	**Karamea**	20 - 1000	2410	11
5	**Mt. Ruapehu**	650 - 1450	2845	9
6	**Urewera**	600 - 1200	2050	10

Map 1. Location of transects.



Map 1. Location of transects.

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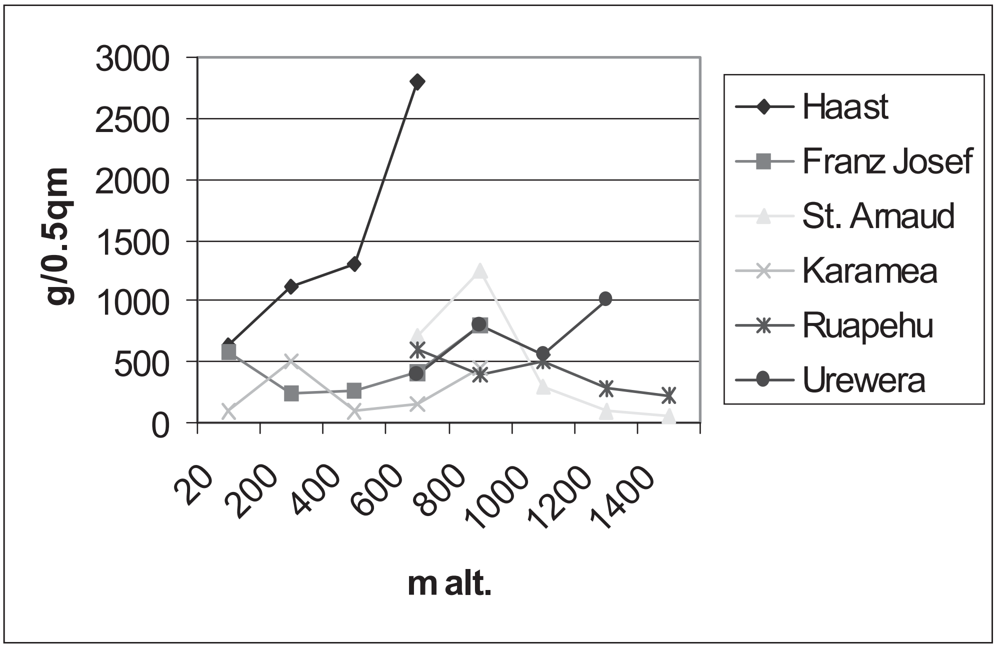

Fig. 2: Phytomass of epiphytic bryophytes (wet weight) in different altitudes along the six transects.

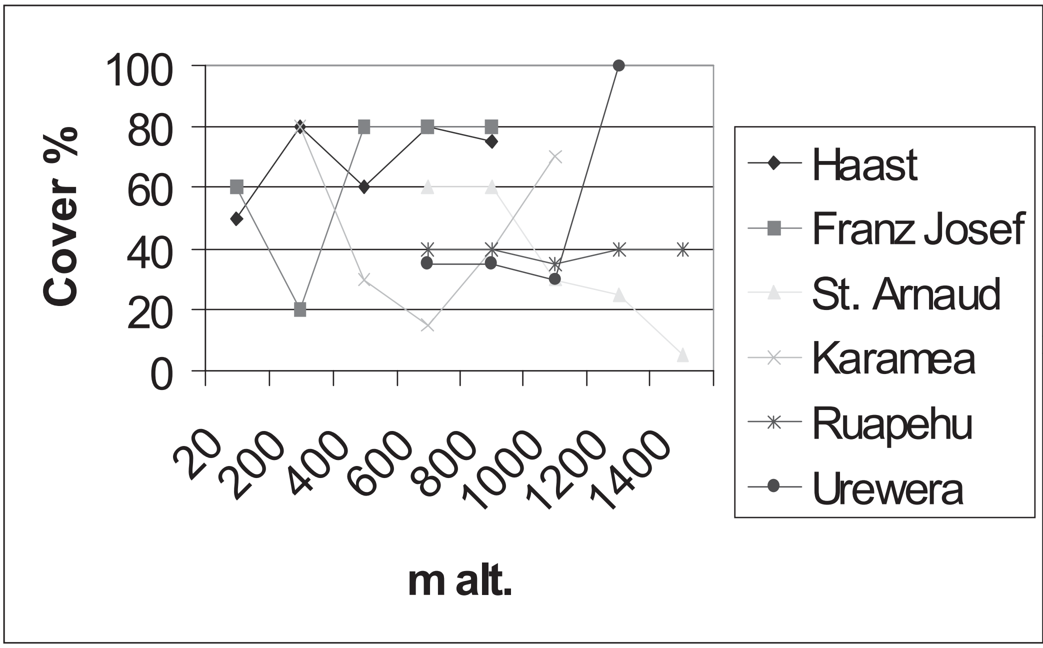

Fig. 3: Cover of epiphytic bryophytes (%) in the relevées along the transects.

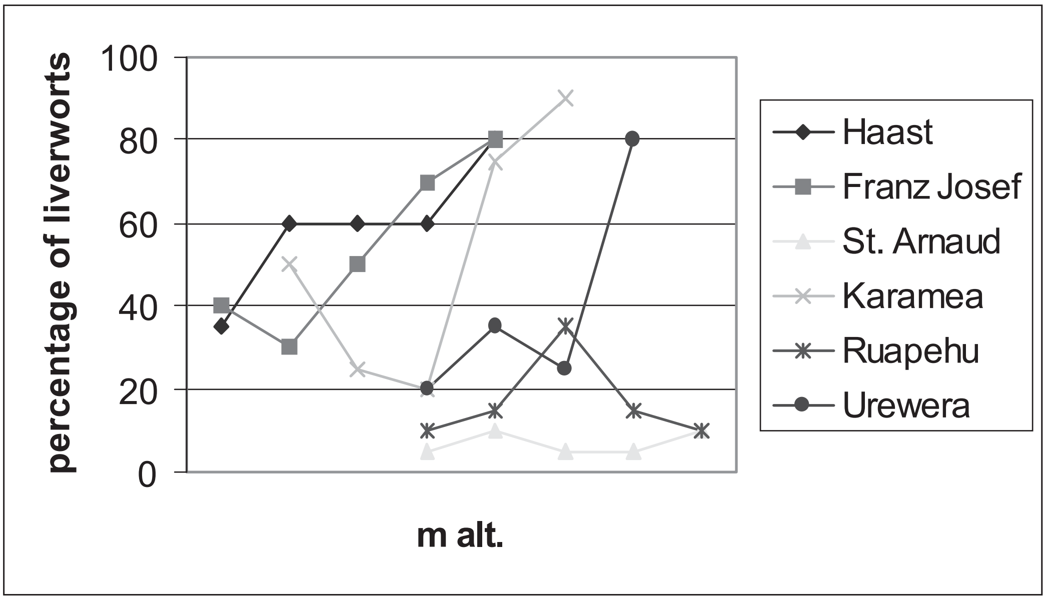

Fig. 4: Percentage of liverworts along the transects.

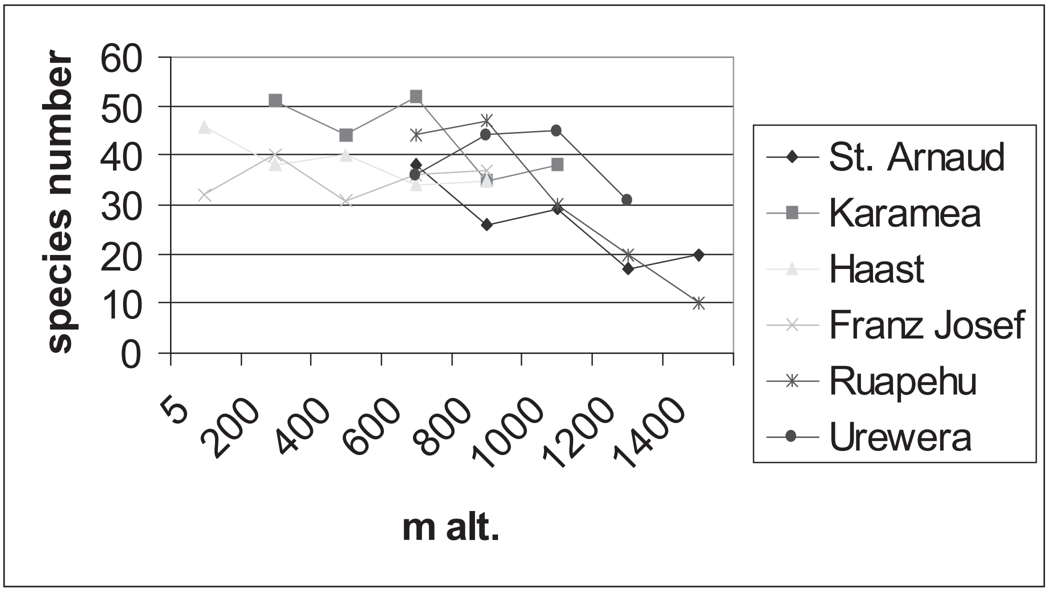

Fig. 5: Species numbers in hectare plots along the altitudinal transects

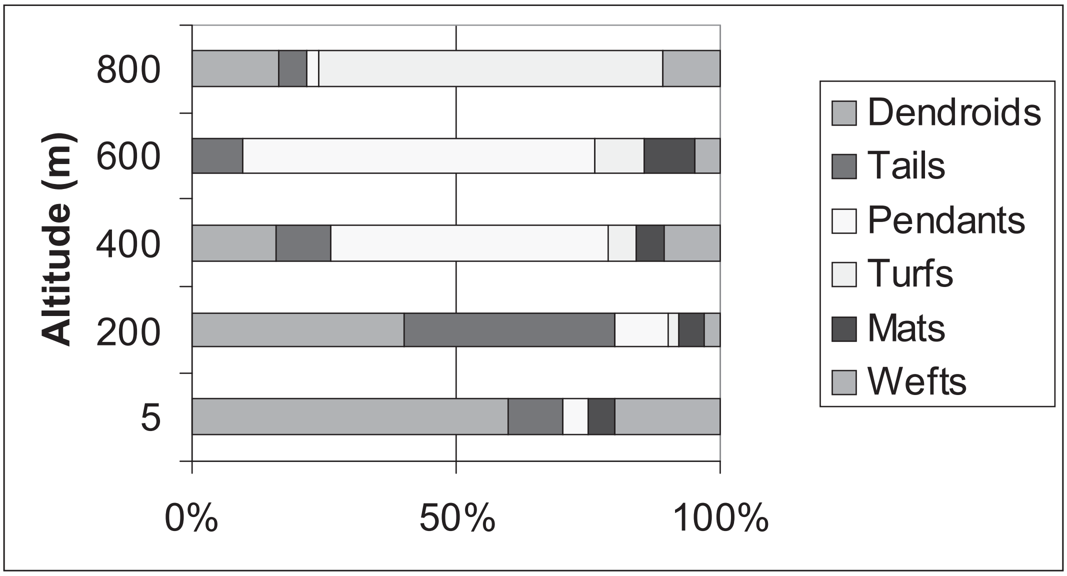

Fig. 6a: Composition of life forms along the Franz-Josef Glacier transect.

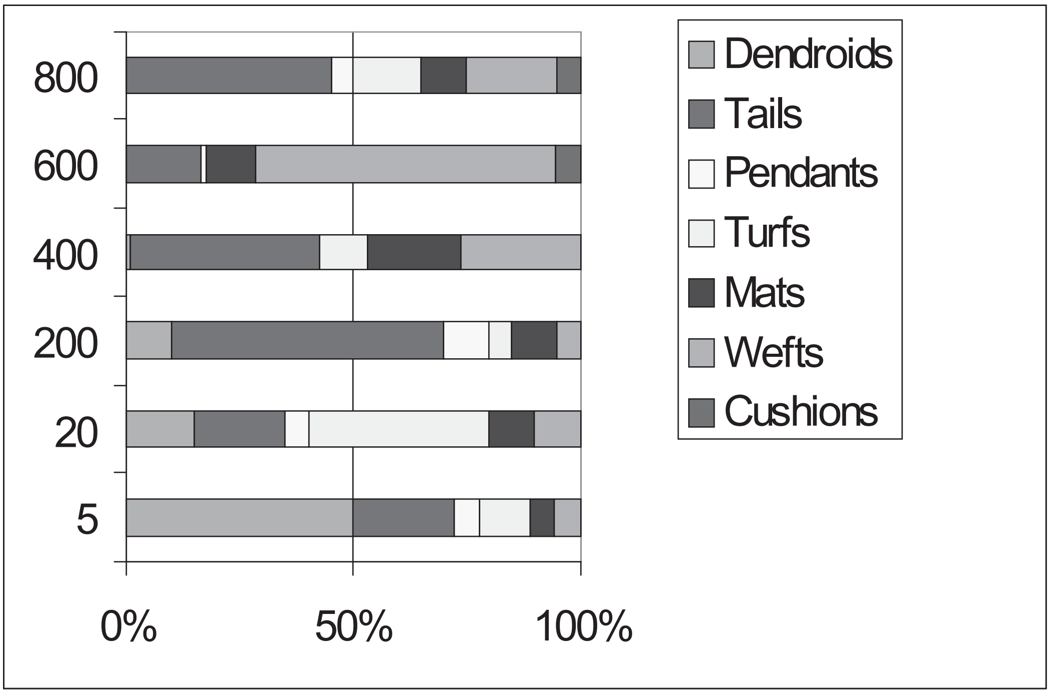

Fig. 6b: Composition of life forms along the Haast transect.

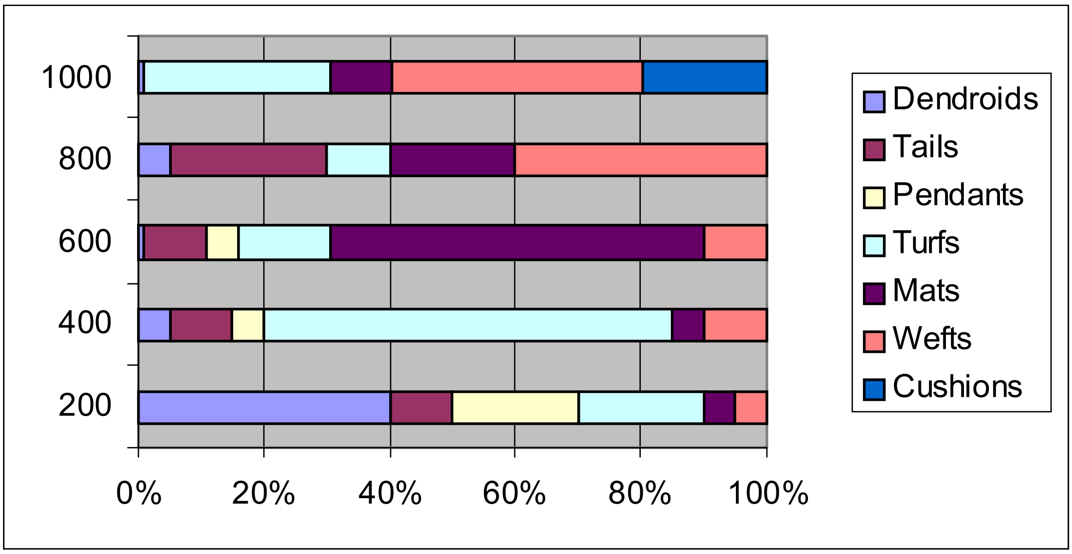

Fig. 6c: Composition of life forms along the Karamea transect.

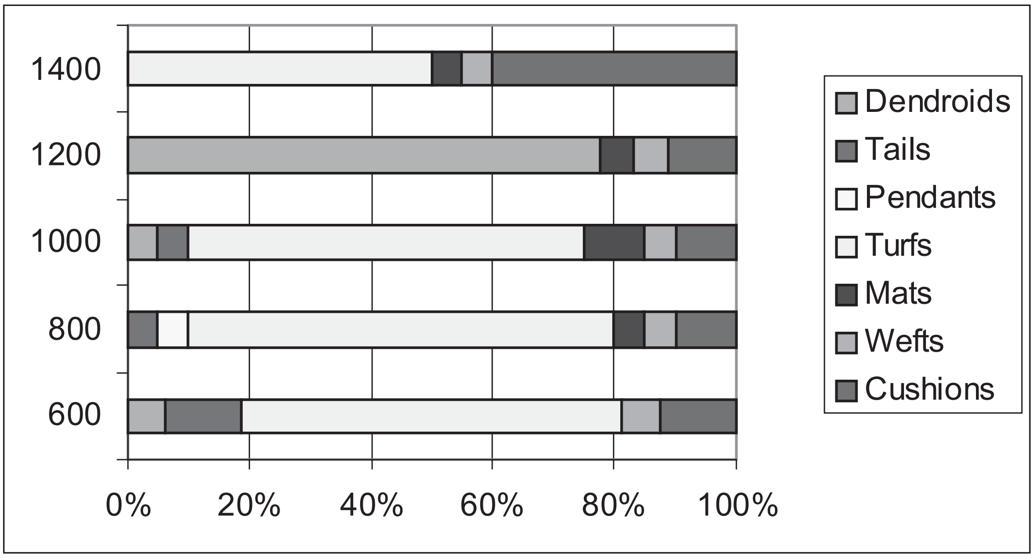

Fig. 6d: Composition of life forms along the St. Arnaud transect.

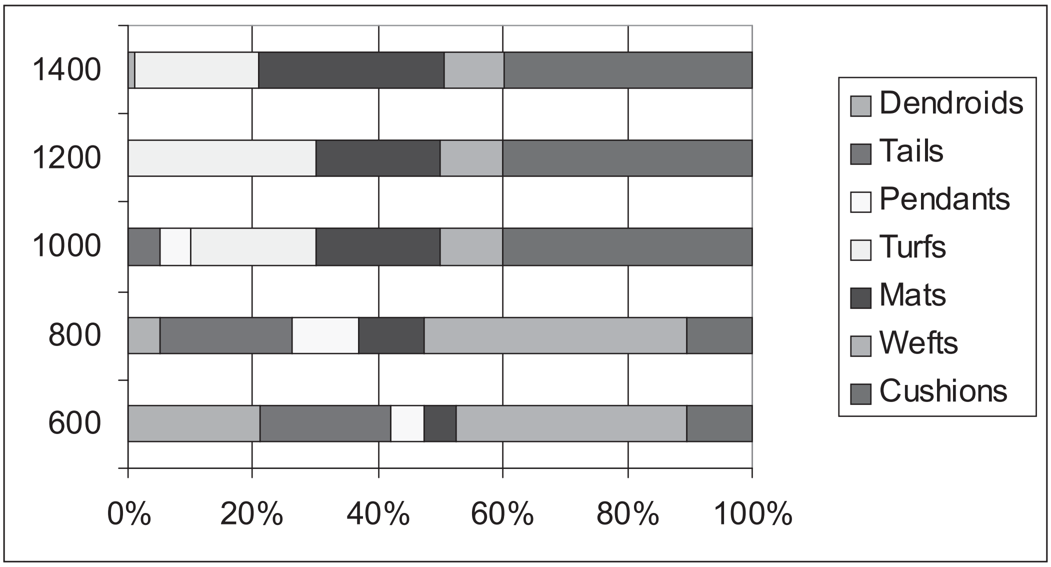

Fig. 6e: Composition of life forms along the Ruapehu transect.

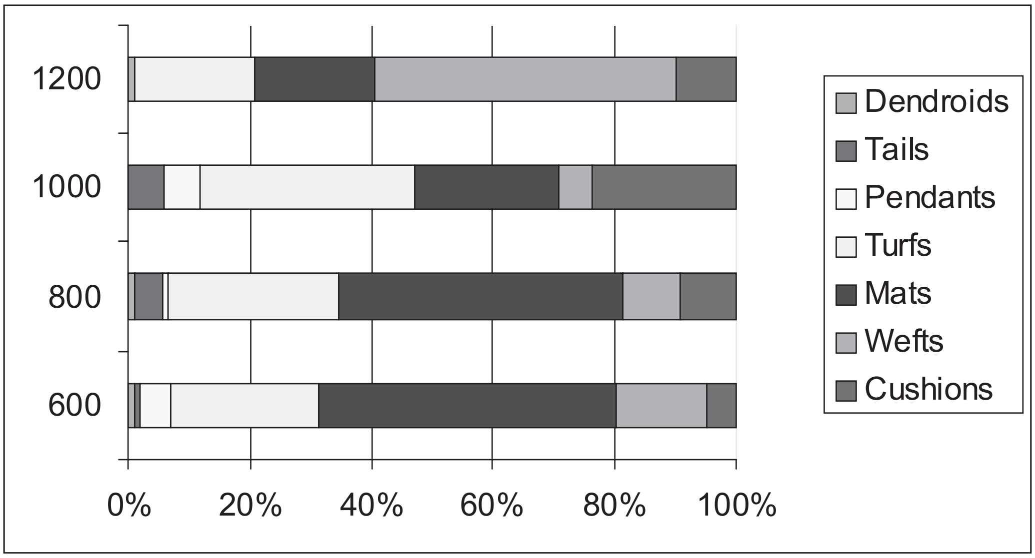

Fig. 6f: Composition of life forms along the Urewera transect.

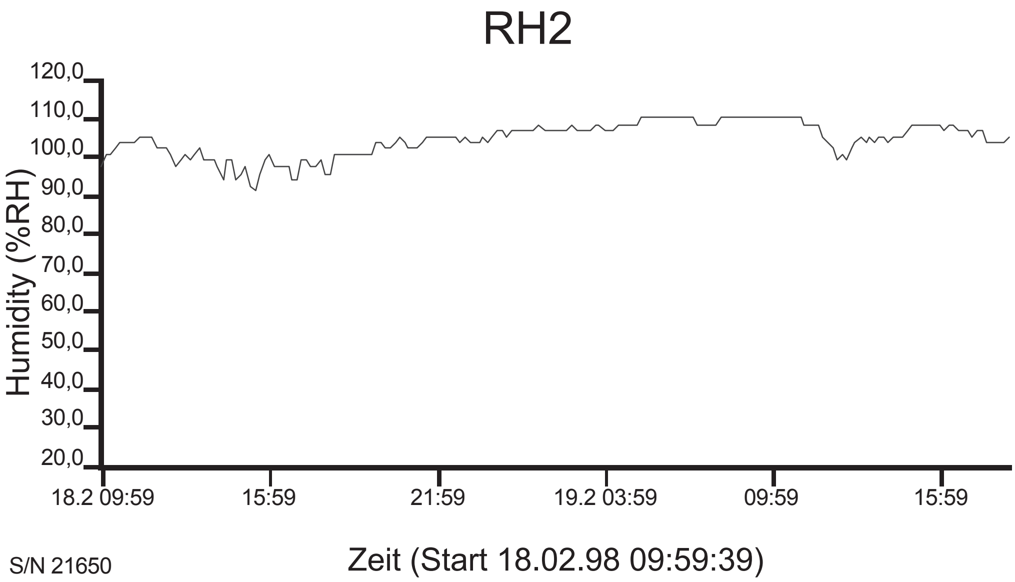

Fig. 7a: Franz-Josef Glacier transect, curve of air humidity in an open (!) site at 200 m alt. Values above 100% are caused by condensation of water on the electrode.

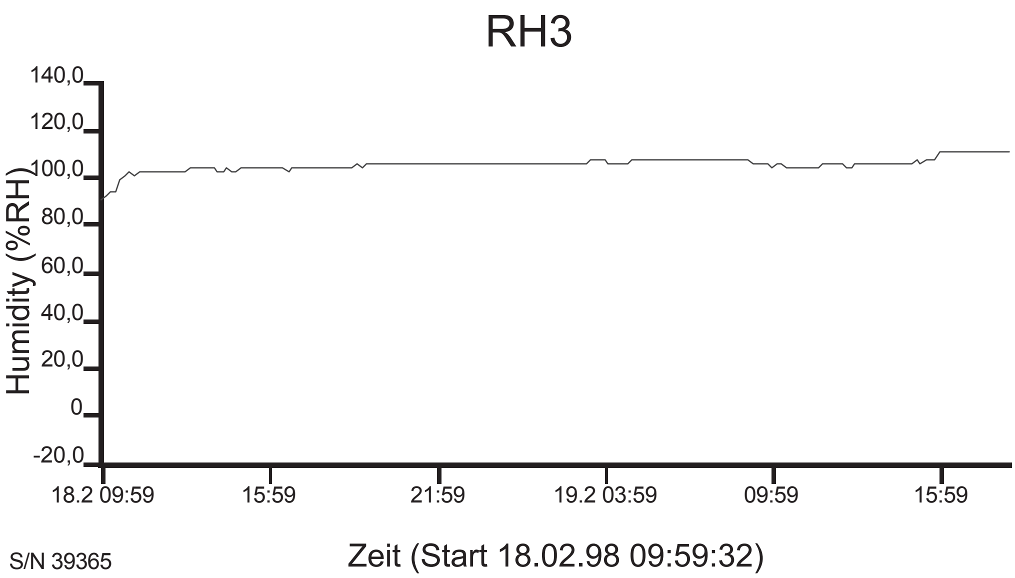

Fig. 7b: Franz-Josef Glacier transect, curve of air humidity in 400 m alt.

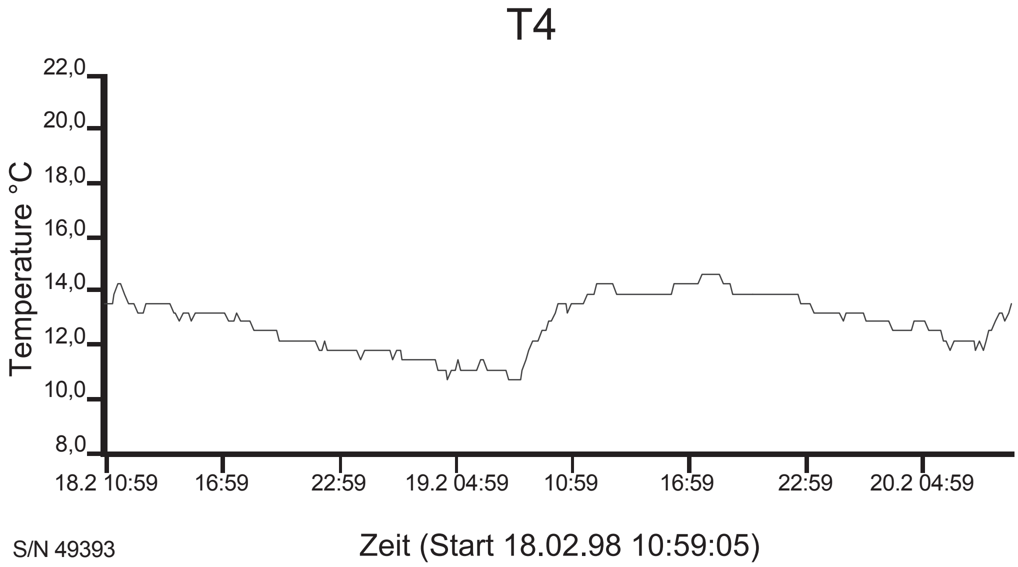

Fig. 7c: Franz-Josef Glacier transect, curve of temperature at 400 m alt.

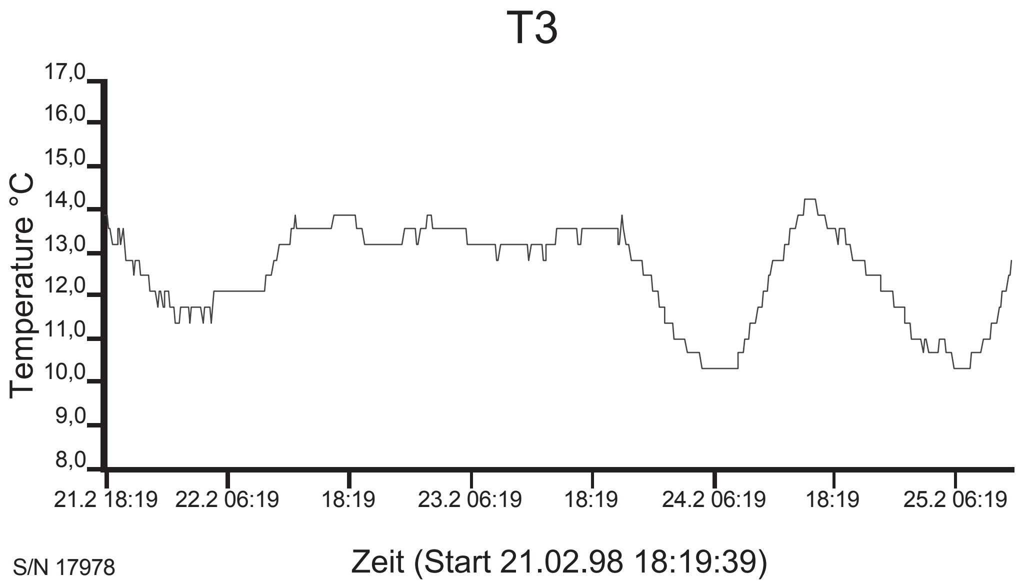

Fig. 7d: Haast Transect. Curve of temperature at 50 m. alt.

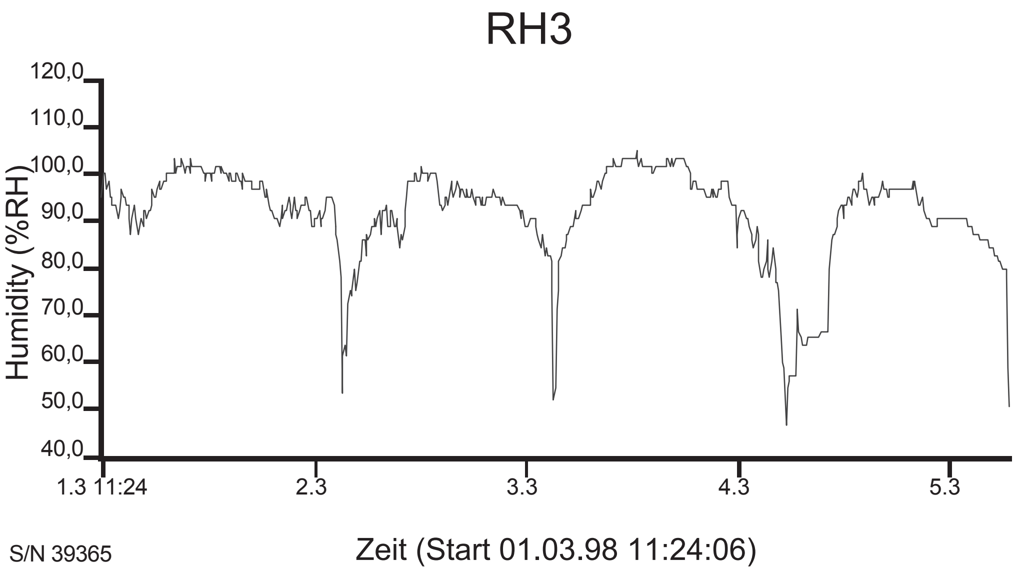

Fig. 7e: Karamea transect. Curve of humidity in 600 m alt.

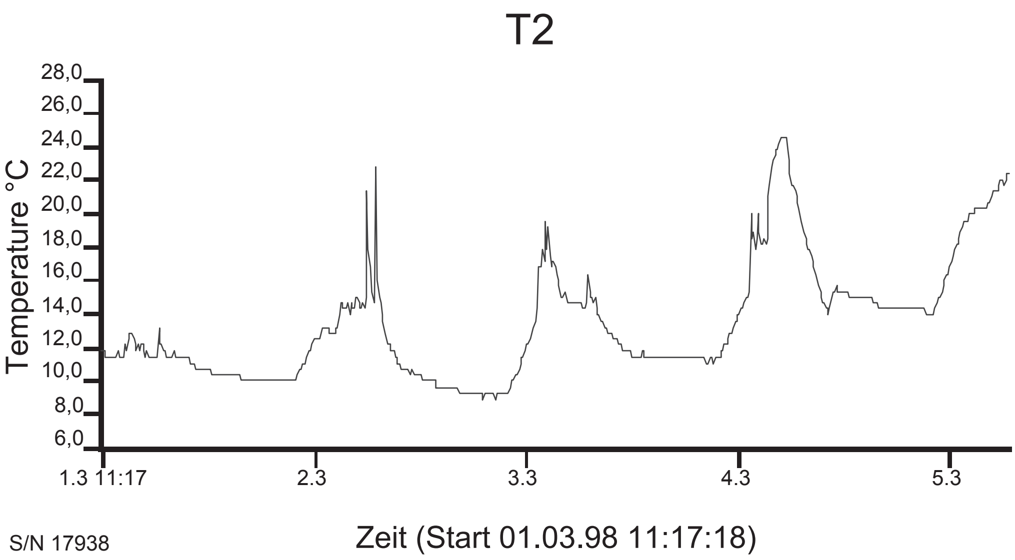

Fig. 7f: Karamea transect. Curve of temperature over a period of five days.

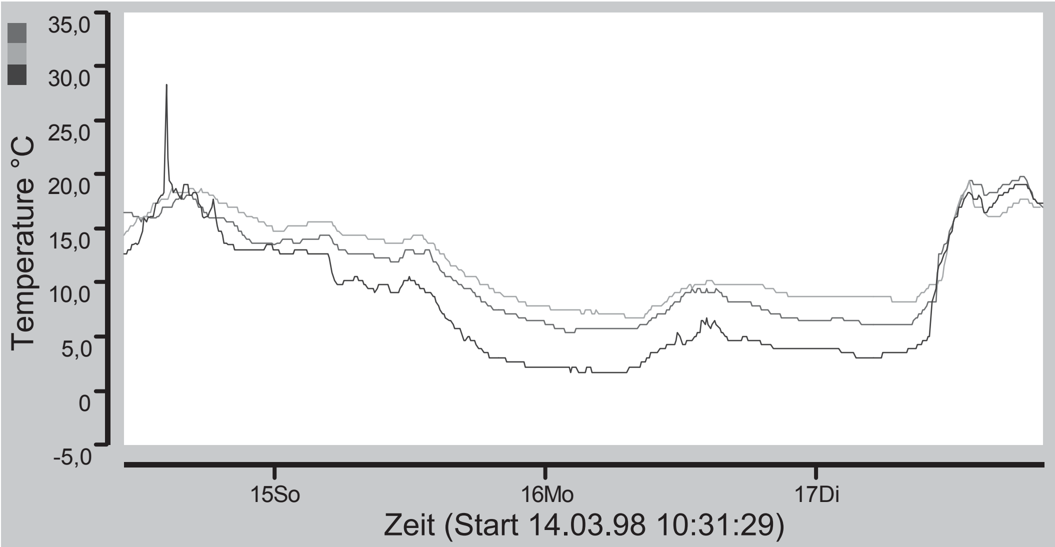

Fig. 7g: Ruapehu-Transect. Curves of temperature in 650, 100 and 1450 m alt.

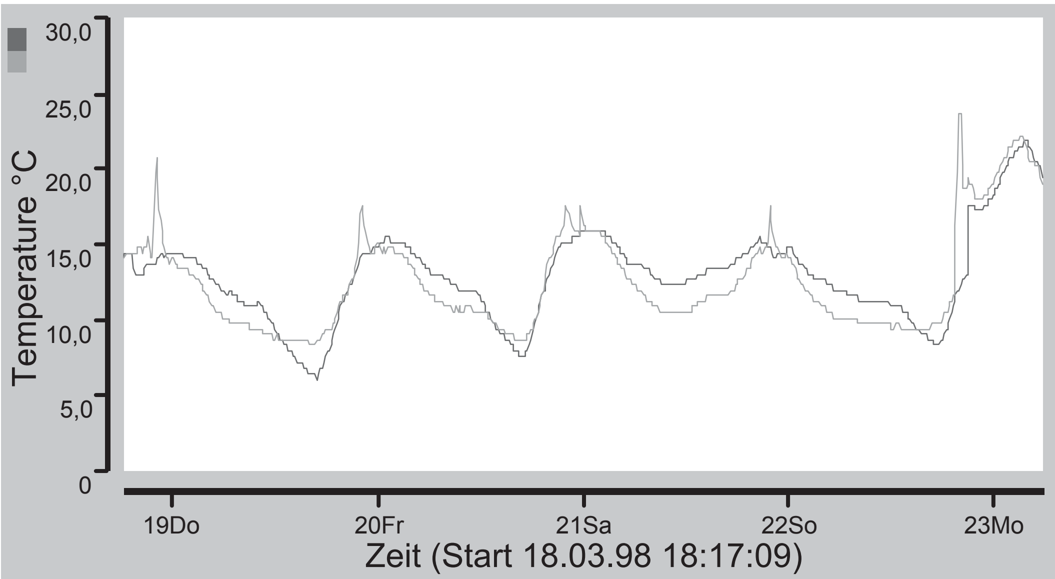

Fig. 7h: Urewera transect. Curves of temperatures in 600 m and 1000 m alt.

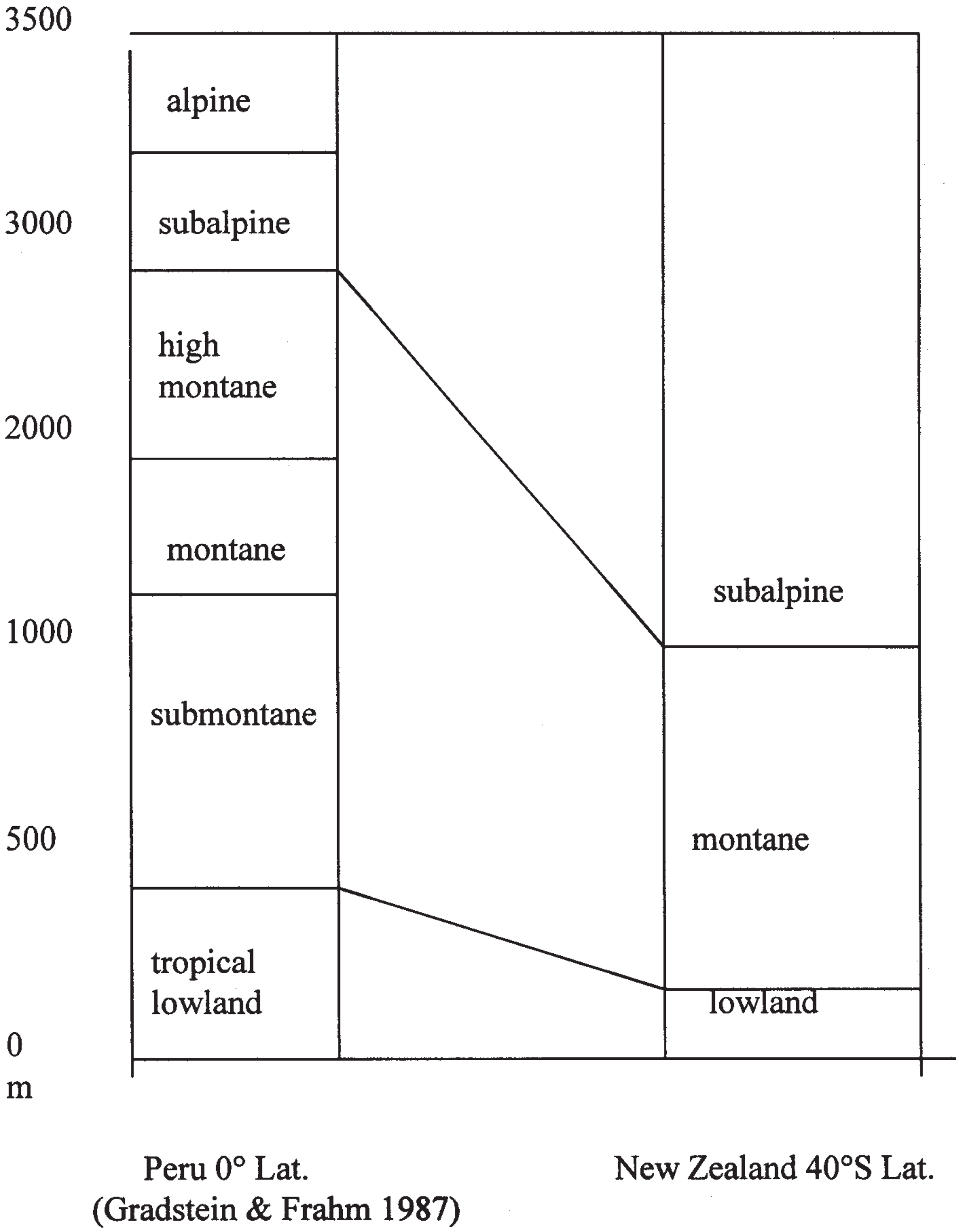

Fig. 8: Comparison of altitudinal zonation of bryophytes in Peru and New Zealand