

Vegetation pattern and soil nutrients of a Magellanic moorland on the Cordillera de Piuchué, Chiloé Island, Chile

Vegetación y nutrientes del suelo en una tundra magallánica en
la Cordillera de Piuchué, Isla Grande de Chiloé, Chile

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ABSTRACT

Magellanic moorlands range from Tierra del Fuego to temperate southern Chile and grow on poorly drained soils, deficient in plant nutrients, leached by high rainfall (2,000 - 6,000 mm/yr). The climate is strongly influenced by the Pacific Ocean to the west. Mean annual temperatures reach 5-6°C. Neither longer frost nor drought periods are frequent.

In Chiloé Magellanic moorland is restricted today to plateaus on the Cordillera de Piuchué, surrounded by scrub and woodland on better drained sites. Palynological studies show that these moorlands are remnants of vaster bog areas covering Chiloé island during the late glacial and early postglacial periods.

A typical moorland complex has different floristic zones. Important ecological factors are the water regime and the nutrient supply. From an ombrotrophic bog center dominated by *Donatia fascicularis*, the vegetation changes to increasingly minerotrophic fen zones with other cushion plants, such as *Astelia pumila*, sedges like *Schoenus antarcticus*, rushes and grasses with a layer of *Sphagnum magellanicum* underneath. The ecotone between moorland and forest is covered by shrubs like *Baccharis magellanica* and *Tepualia stipularis*.

The nutrient supply of the moorland was characterized by the total and plant-available contents of K, Na, Ca, Mg, Fe, Mn and Al as well as the C/N ratio and the effective cation exchange capacity (CEC) of the peat soils. The results show that only the cushion bog of *Donatia* has nearly ombrotrophic conditions, whereas the *Astelia* mire and the *Schoenus* fen are strongly influenced by mineral seepage water. In addition to nitrogen, which could not be investigated in this study, phosphorus is the most important limiting factor for moorland vegetation.

Man has disturbed the fragile equilibrium between woodland and moorland, by fire and logging. The enhanced runoff from deforested woodland favors the invasion of some moorland plant species.

Key words: Bog-fen zonation, mineral nutrition, Chilean coastal range, succession.

RESUMEN

Las tundras Magallánicas se extienden desde Tierra del Fuego (55°S) hasta el sur templado de Chile (40°S). Se desarrollan en suelos anegados, pobres en nutrientes y lavados por lluvias abundantes (2,000-6,000 mm/a). El clima está influido fuertemente por el Océano Pacífico al oeste. Las temperaturas medias anuales alcanzan 5-6°C. Ni períodos de heladas ni de sequía son frecuentes.

En Chiloé, las tundras magallánicas están restringidas actualmente a las cumbres y las laderas occidentales de la Cordillera de Piuchué. Estudios palinológicos demuestran que estas turberas son relictos de formaciones más extensas que cubrieron la Isla de Chiloé durante el período glacial y postglacial.

Un complejo típico de tundra está compuesto de zonas diferentes en composición florística y condiciones ecológicas. Los factores más importantes son los regímenes hídricos y de nutrientes. La vegetación cambia de una turbera central ombrotrofica, formada por *Donatia fascicularis* a zonas turbosas de creciente influencia minerotrofica con otras plantas en cojín como *Astelia pumila*, con Ciperáceas como *Schoenus antarcticus*, juncos y pastos sobre un estrato de *Sphagnum magellanicum*. El ecotono entre la turbera y el bosque está cubierto de arbustos como *Baccharis magellanica* y *Tepualia stipularis*.

Las turberas se caracterizaron por los contenidos totales y disponibles de K, Na, Ca, Mg, Fe, Mn and Al, además de la relación C/N y la capacidad efectiva de intercambio de cationes de sus suelos. Los resultados muestran que solamente la turbera de *Donatia* tiene condiciones casi ombrotroficas. En cambio la zona de *Astelia* y la de *Schoenus* están bajo la influencia de aguas subterráneas provenientes de suelos minerales. Aparte del nitrógeno, que no ha sido estudiado en este trabajo, el factor limitante para la vegetación de las turberas es el fósforo.

El hombre ha alterado el frágil equilibrio entre bosques y turberas, destruyendo los bosques con fuego y extrayendo madera. El escurrimiento superficial desde áreas taladas favorece la invasión de algunas especies de turberas.

Palabras claves: Turberas, composición florística, factores limitantes, zonación, sucesión.

INTRODUCTION

The Magellanic moorland (Dollenz 1980, Moore 1979, 1983, Pisano 1983) is the typical plant formation of western Patagonia and the subantarctic island. Its characteristic vegetation is cushion-plant bogs or cushion-plant mires. These formations are restricted to areas of the southern hemisphere influenced by strong winds coming from the oceans. Floristically similar plant formations exist in New Zealand, Tasmania and Southeast Australia (Godley 1960, 1978).

In southern Chile, Magellanic moorland occurs along with evergreen subantarctic rainforests of *Pilgerodendron uviferum*, *Nothofagus betuloides* and *Drimys winteri*, from the strait of Magellan to the Golfo de Penas (e.g. Dusen 1903, Scottsberg 1916, Schmithüsen 1956). Isolated areas of moorland vegetation occur farther north, e.g. on Chiloé Island and on the coastal range of southern Chile (Fig. 1), the Cordillera Pelada (Ramírez 1968) and Cordillera de Nahuelbuta (Looser 1952).

The flora of the moorland formation changes from 56°S to 40°30'S. Its composition in Chiloé Island is still quite similar to the Patagonian moorland. Most of the typical cushion plants which dominate these mire formations in Tierra del Fuego are found here: *Donatia fascicularis* (Donatiaceae), *Astelia pumila* (Liliaceae), *Gaimardia australis* (Centrolepidaceae), *Oreobolus obtusangulus* (Cyperaceae). *Gaimardia* and *Oreobolus* grow in similar mire formations also in Parque Nacional Vicente Pérez Rosales (Villagrán 1980).

As cushion-plant mires and bunch-sedge lawns grow in contact with vegetation of swampy and alluvial sites, as well as with woodland vegetation on dryer soils, they form mixed communities with plants of these formations.

The aims of this investigation were to describe the vegetation and soils of a cushion-plant mire and its accompanying plant formations, including forest-moorland transitions and to explain the vegetation zonation by studying the most important features of its mineral nutrition.

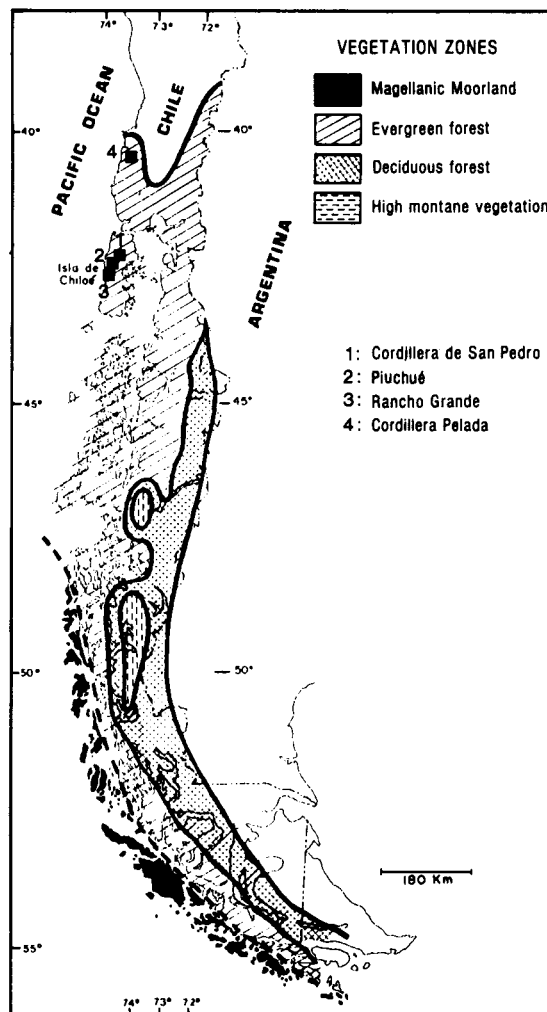


Fig. 1: Distribution of the Magellanic moorland, the evergreen rainforest and the summergreen broad-leaf forest in southern Chile (after Schmithüsen 1956 and Moore 1983, from Villagrán 1988). Location of the study area on Chiloé.

Distribución de las tundras magallánicas, el bosque lluvioso siempreverde y el bosque latifoliado y caducifolio en Chile austral (según Schmithüsen 1956 y Moore 1983, de Villagrán 1988). Localización del área de estudio en Chiloé.

STUDY AREA

The striking constancy of the flora and vegetation of the Magellanic moorland along its wide geographical range must have its origin in a common history (Villagrán 1988) and similar ecological conditions prevailing until today. Typical examples of this vegetation type are bound to extremely oceanic areas with 2,000 -

6,000 mm precipitation evenly distributed during the year. Mean annual temperatures reach 5° to 6°C with little difference between the cool summer and the moderately cold winter periods. Its local distribution is restricted to wet, poorly drained plains, with a bed-rock poor in bases and mineral nutrients in general (Holdgate 1961, Pisano 1983, Roig 1984).

Magellanic moorland in Chiloé is confined to the uplands (700 m) and the western slopes of the Cordillera de Piuchué. This mountain range represents the southern extension of the Chilean coastal range, with a basement of Precambrian and/or paleozoic extremely metamorphic schists (Zeil 1964, Saliot 1969, Watters a. Fleming 1972). These schists consist of quartzitic fieldspates, penetrated by green schists richer in mineral nutrients.

The Cordillera de Piuchué forms a very effective climatic boundary. Whereas the western slopes are exposed to the offshore winds coming from the Pacific, the eastern slopes are more protected. Although long ranging climatic information is unavailable for this area (Holdgate 1961, Villagrán 1988), estimates of over 3,000 mm per year have been made in the uplands. As these mountains are very often covered by clouds, additional fog deposition can be expected. The precipitation is evenly distributed over the year and during the winter there are occasional snowfalls. During summer (december to february), occasionally longer dry and warm periods may occur.

In the area of the moorlands, the mean annual temperature may seldom be above 5° - 6°C. Frosts can occur in the uplands at any time of the year. Periods with night frost and temperatures above zero during the day may happen in combination with short droughts.

Due to the geological and climatological conditions, most of the soils of the Cordillera de Piuchué are poor in bases, influenced by standing or seeping water. They have an upper peat layer of varying depth. Therefore podzolic acid anmoor and moor gleys are predominant. In these soils, humic substances, manganese, iron and perhaps aluminium are mobile and

can be transported along the soil profile or leached. An iron-enriched layer was observed frequently on top of the bedrock. Podsollic brown soils are found on better drained slopes (Pérez C., personal communication 1989).

The altitudinal vegetation belts reflect clearly the prevailing climate and soil conditions (Villagrán 1985). Due to lower precipitation and higher radiation, the different forest communities reach their upper limits at 50 to 100 m higher levels on the eastern slopes than on the western slopes. The moorland is restricted to the uplands above 600 m and to the western slopes, where they may descend 150-200 m.

Following an east-west transection at about 42°20'S, grow in contact with forests dominated by *Nothofagus nitida*, *Amomyrtus luma* and *Drimys winteri*, occasionally mixed with *Saxegothaea conspicua* and *Podocarpus nubigena*. These forests are restricted to steeper slopes. Small patches of *Nothofagus betuloides* and *N. antarctica* are found within the moorland (Fig. 2). In the ecotone between the forest and the open moorland we find shrub formations of *Baccharis magellanica*, *Chusquea uliginosa*.

The western slopes are cut up by deep valleys. Thus narrow ridged alternate with



Fig. 2: Moorland on the Fundo Pichihué on the Cordillera de Piuchué/Chiloé with cushion-plant bogs surrounded by sedge/grass fen and islands of *Nothofagus* woodland.

Turberas en el Fundo Pichihué en la Cordillera de Piuchué/Chiloé, con formaciones de plantas en cojín rodeadas de turberas dominadas por ciperáceas y gramíneas y grupos aislados de *Nothofagus*.

less inclined slopes interrupted by broad terraces. Sites with extremely different moisture and temperature regime are found side by side. The cushion-plant formations cover flat areas or slightly inclined terraces (Fig. 3) down to about 450 m. They are frequently surrounded by open forests of *Fitzroya cupressoides* and *Pilgerodendron uviferum*. The ecotone is dominated by *Tepualia stipularis*. This species also occurs in the understory of open conifer forests. Cushion-plant mires always coincide with the poorest drained sites.



Fig. 3: Moorland terrace on the western slope of the Cordillera de Piuchué covered with a cushion-plant carpet and *Schoenus antarcticus* bunches. In the foreground a wind-shaped *Nothofagus* tree.

Terraza en la ladera occidental de la Cordillera de Piuchué cubierta de una turbera con un césped de plantas en cojín y macollos de *Schoenus antarcticus*. En primer plano un árbol de *Nothofagus* doblado por el viento oeste.

METHODS

A typical sequence from the center of a cushion bog community to the surrounding forest was selected (Fig. 4). Following this 130 m long transect line the vegetation was sampled in 1 x 1 m quadrats, 1-3 m apart. The percent cover of each species was estimated as precisely as possible in each quadrat. The nomenclature follows Marticorena & Quezada (1985). The transect was permanently marked to repeat this description in the coming future.

At five locations along the transect, soil profiles were dugged down to 40 or 50 cm

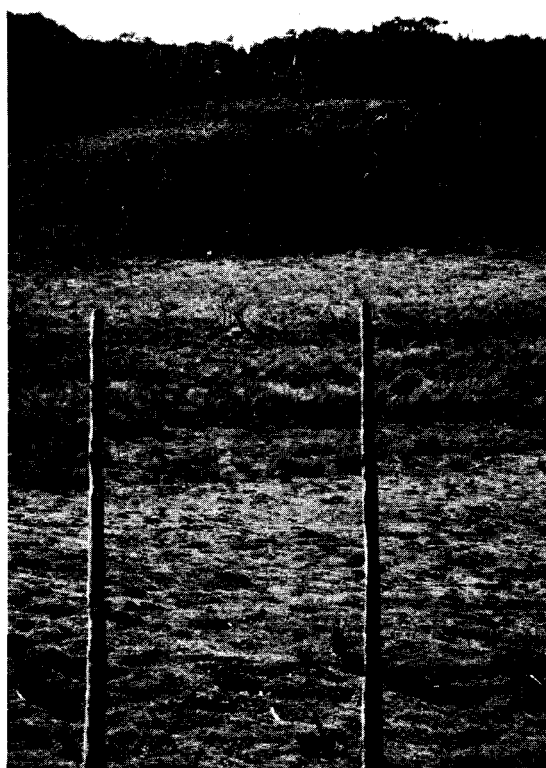


Fig. 4: Vegetation transect on the Fundo Pichihué (Cordillera de Piuchué/Chiloé). In the foreground the cushion-plant bog of *Donatia*, in the middle the depression with *Astelia* cushions, in the background the *Schoenus antarcticus* fen and the *Nothofagus* woodland.

Transecta estudiada en el Fundo Pichihué (Cordillera de Piuchué/Chiloé). En primer plano la turbera formada por *Donatia*, en el centro una depresión con cojines de *Astelia*, al fondo la formación de *Schoenus antarcticus* y el bosque de *Nothofagus*.

depth. Soil samples were collected from two layers, 0-10 cm and 20-30 cm. Big roots were eliminated in the field. Soil samples were air-dried and screened through a sieve with 2 mm-mesh wire.

The following chemical analyses were carried out in the laboratory (at University of Trier, Germany):

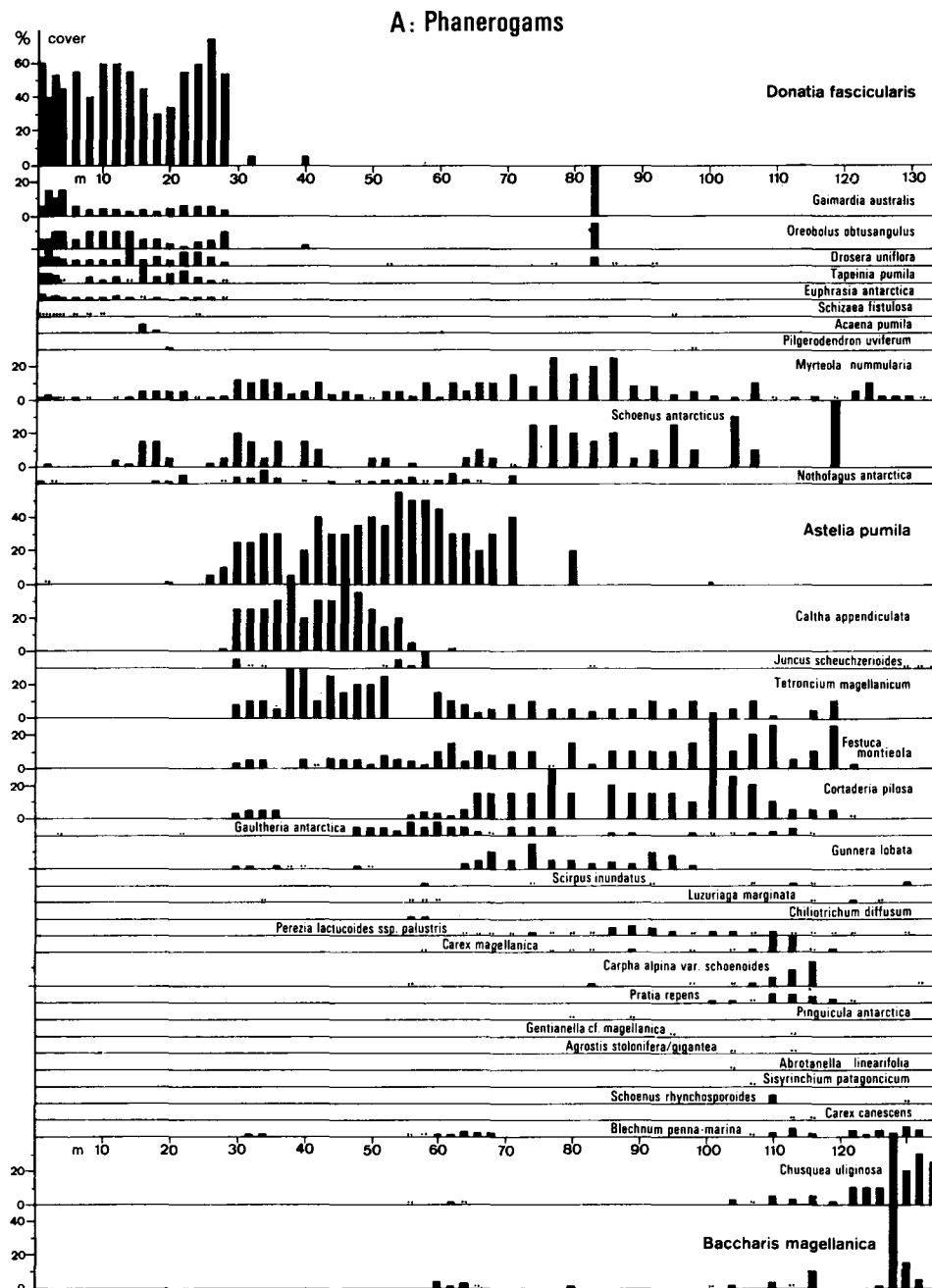
Determination of the total contents of C and N: Element analyzer CHN-O-Rapid (Heraeus). Total contents of P: Extraction with HNO_3 , in pressure bombs and colorimetric determination (Wenzel 1956). Total contents of K, Mg, Ca, Mn, Fe, Al: Extraction with HNO_3 in pressure bombs and determination with an AAS.

Determination of the plant-available amounts of P and K: Extraction with ammonium-lactate-acetic-acid following the method of Egner-Riehm (Schilchting & Blume 1966). Determination of the exchangeable fractions of the cations (effective cation exchange capacity = CEC_{eff}) by extraction with NH_4Cl and determination of the elements with an AAS. Calculation of the H-ions following Nair & Prenzel (1978) and Meiwes *et al.* (1984).

RESULTS

Vegetation pattern of a typical moorland zonation

The moorland occurs on flat lands, broad shallow depressions and slightly inclined slopes. The vegetation of the central cushion-plant bogs (Fig. 5: 1-30 m) is characterized by a dense carpet of *Donatia fascicularis*, *Gaimardia australis* and *Oreobolus obtusangulus*. These species are



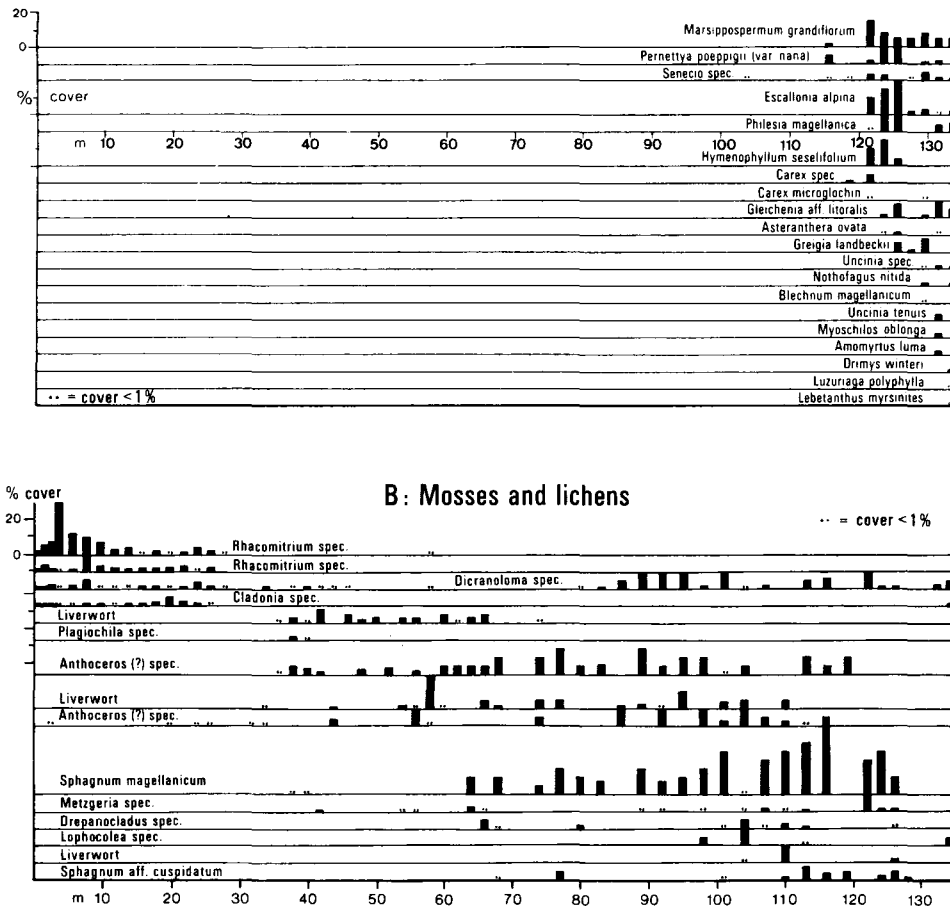


Fig. 5: Vegetation zones of a typical moorland on an upland plateau of the Cordillera de Piuchué/Chiloé at about 700 m: 0-28 m = *Donatia fascicularis* bog, 28-71 m = *Astelia pumila* mire, 71-119 m = *Schoenus antarcticus*/*Festuca monticola*/*Cortaderia pilosa* fen, 119-134 m = *Baccharis magellanica*/*Chusquea uliginosa* scrub. Part A: Phanerogams, Part B: Mosses and lichens (incomplete species list). Height of the columns: % vegetation cover. Sample plots 1 x 1 m.

Zonas de vegetación de una turbera típica en una planicie de altura en la Cordillera de Piuchué/Chiloé en alrededor de 700 m: 0-28 m = turbera de *Donatia fascicularis*, 28-71 m = turbera de *Astelia pumila*, 71-119 m = turbera de *Schoenus antarcticus*/*Festuca monticola*/*Cortaderia pilosa*, 119-134 m = matorral de *Baccharis magellanica*/*Chusquea uliginosa*. Parte A: Fanerógamas, Parte B: Musgos y líquenes (lista incompleta). Altura de las columnas: Cubierta de vegetación en %. Tamaño de las parcelas: 1x1 m.

accompanied by few dwarf herbs, such as *Drosera uniflora*, *Tapeinia pumila*, *Euphrasia antarctica*, *Schizaea fistulosa*, *Myrteola nummularia* and typical mosses and lichens of the genus *Rhacomitrium*, *Dicranoloma*, and *Cladonia*.

Often, *Schoenus antarcticus*-bunches and occasional stunted *Nothofagus antarctica*-trees appear at the margins of the *Donatia*-carpets.

The sharp boundary between the moorland dominated by *Donatia* and that dominated by *Astelia pumila* (Fig. 5:

30-71 m) coincides with a narrow depression bordering the *Donatia* bog. The effect of the minerotrophic seepage water becomes obvious due to the association with swamp plants, such as *Caltha appendiculata* and *Tetroncium magellanicum*. The conditions of minerotrophic fen areas are also indicated by the grasses *Festuca monticola* and *Cortaderia pilosa*.

Astelia is not restricted to sites with permanently seeping ground water. This is proved by the fact that, without *Caltha* and little coverage of *Tetroncium*, *Astelia*

can have high dominance (40-50% cover) in the moorland (Fig. 5: 54-61 m).

Beyond the *Astelia*-carpet the ground starts rising to the base of a steeper slope covered with woodland. Here the lowest field layer is composed by *Myrteola nummularia*, *Tetroncium magellanicum*, *Gaultheria antarctica* and *Gunnera lobata*. Above them the leaves and shoots of *Schoenus antarcticus*, *Festuca monticola* and *Cortaderia pilosa* emerge up to 20-30 cm high (Fig. 5: 73-108 m). A moss layer of *Sphagnum magellanicum* covers 30-60% of the soil. Some species appear only near the shrub belt. These are *Carex magellanica*, *Carpha alpina* var. *schoenoides*, *Pratia repens*, *Schoenus rhynchosporoides*, *Carex canescens* and a species of *Sphagnum* (Fig. 5: 108-120 m). Some elements such as *Blechnum penna-marina*, *Chusquea uliginosa* and *Baccharis magellanica* are common to open scrub and forest margins.

The ecotone between open moorland and forest has variable lengths. In the selected transect, this zone is about 15 m wide (Fig. 5: 120-134 m). Some dead trees are standing between the dense shrub layer formed by *Baccharis magellanica*,

Chusquea uliginosa, *Escallonia alpina* and *Philesia magellanica*. The herb layer, clearly indicates the relation to the adjacent forest (Table 1). Poorly growing trees of *Nothofagus nitida* and *Amomyrtus luma* are also present.

Moorland soils

The uplands of Piuchué, with the exception of few rocky outcrops are covered with moor- and anmoor-gleys, in which the water table surfaces nearly all year round. The upper peat layer is normally 10 cm deep (Holdgate 1961).

The soil profiles and the total contents of C and N (Fig. 6), indicate that the soils below the *Donatia*-, *Astelia*- and *Schoenus*-vegetation are moor-gleys, under *Baccharis*-scrub have the character of an anmoor-gley, and under *Nothofagus*-forest that of a gley. At the time of sampling, all soils were very moist up to the top layer.

Peat layers are moderately to strongly decomposed and the degree of decomposition increases with depth. This agrees with the rising N_t-contents and the decreasing C/N-ratio (Fig. 6). The highest C/N-ratio (35) was found in the *Astelia*-plot.

TABLE 1

Floristic composition of the forest on the SW-exposed slope at the end of the vegetation transect
Composición florística del bosque sobre la ladera suroeste al final de la transecta estudiada

	Cover of the tree layer	(T): 75%,	height: 6-8 m			
	Cover of the shrub layer	(S): 60%,	height: 2 m			
	Cover of the field layer	(F): 10%,	height: 0,30 m			
T:	50%	<i>Drimys winteri</i>		F:	5%	<i>Gleichenia litoralis</i>
	20%	<i>Nothofagus nitida</i>			5%	<i>Juncus cf. chilensis</i>
	5%	<i>Desfontainia spinosa</i>			5%	<i>Uncinia spec.</i>
	+	<i>Pilgerodendron uviferum</i>			5%	<i>Drimys winteri</i>
	+	<i>Embothrium coccineum</i>			5%	<i>Desfontainia spinosa</i>
	+	<i>Podocarpus nubigena</i>			5%	<i>Escallonia alpina</i>
S:	30%	<i>Chusquea quila</i>			5%	<i>Baccharis magellanica</i>
	10%	<i>Gaultheria phyllyreifolia</i>			5%	<i>Luzuriaga poliphylla</i>
	10%	<i>Philesia magellanica</i>			5%	<i>Greigia landbeckii</i>
	5%	<i>Desfontainia spinosa</i>			5%	<i>Philesia magellanica</i>
	3%	<i>Nothofagus nitida</i>		Epiphytes:		
	2%	<i>Drimys winteri</i>				<i>Philesia magellanica</i>
	+	<i>Blechnum magellanicum</i>				<i>Serpyllopsis caespitosa</i>
	+	<i>Escallonia alpina</i>				<i>Hymenophyllum pectinatum</i>
						<i>Hymenophyllum peltatum</i>
						liverworts, mosses, lichen

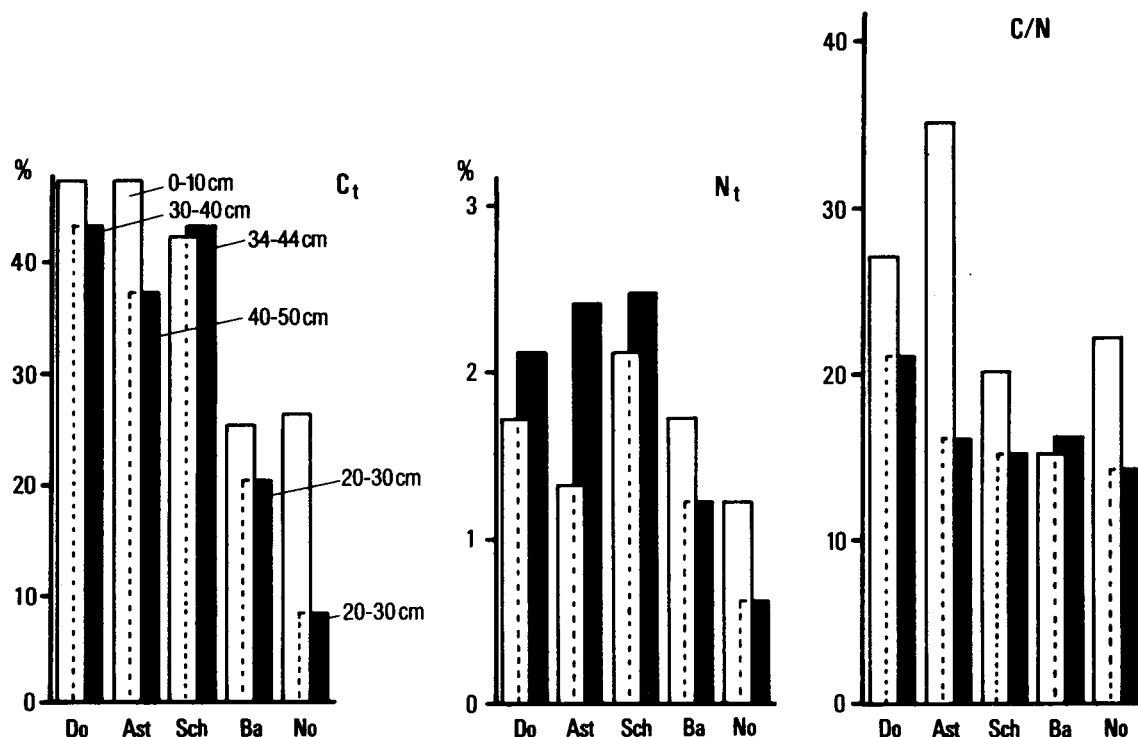


Fig. 6: Total contents of carbon (C_t) and nitrogen (N_t) and C/N ratios in the soil of typical vegetation zones from the moorland transect. C and N in % of dry soil from two soil depths. Do = *Donatia* bog, Ast = *Astelia* mire, Sch = *Schoenus* fen, Ba = *Baccharis* scrub, No = *Nothofagus* forest.

Contenido total de carbono (C_t) y nitrógeno (N_t) y proporción C/N en el suelo de zonas típicas de la transecta de turberas. C y N en % de suelo seco de dos capas. Do = *Donatia*, Ast = *Astelia*, Sch = *Schoenus*, Ba = *Baccharis*, No = *Nothofagus*.

The difference with the lower soil layer is here the greatest of all profiles.

In addition to moisture, nutrient availability in the rooted soil layer is the most important factor influencing the floristic composition of the moorland vegetation. One can separate the basic nutrients, including K, Ca, and Mg, from occasionally mobile toxic elements like Fe, Mn or Al, and mineral P and N otherwise bound in organic compounds.

The availability of these elements is modified by the pH, the redox-potential and the presence of other substances which form insoluble compounds with them. In the present investigation the redox-potential and the availability of mineral N could not be determined in the field because of technical reasons.

The effective cation exchange capacity (CEC_{eff} , circle-shaped diagrams in Fig. 7 and 8) is always higher in the upper 10

cm than in the deeper soil layer. The differences between the two layers are larger in the *Donatia*- and *Astelia*-plots. The densely rooted top soil has between 4.5 to 2.8 times the CEC of the deeper soil, which is saturated with water all year. Especially striking is the high cation saturation in the upper 10 cm of the *Astelia* peat (298 meq/kg dry soil). Small differences are not considered, because only mixed soil samples without replicates were analyzed.

The exchangeable cation contents of the lower soil layer indicate a possible influence of underlying mineral soils or seepage water. They are lowest under the *Donatia*-bog (Fig. 7). There was a higher availability of K, Na, Mg and Fe in the lower soil layer of the *Astelia* plot. Mn can be found in all samples only in traces. The Al values increase from the center of the moorland to its border, reflecting the ex-

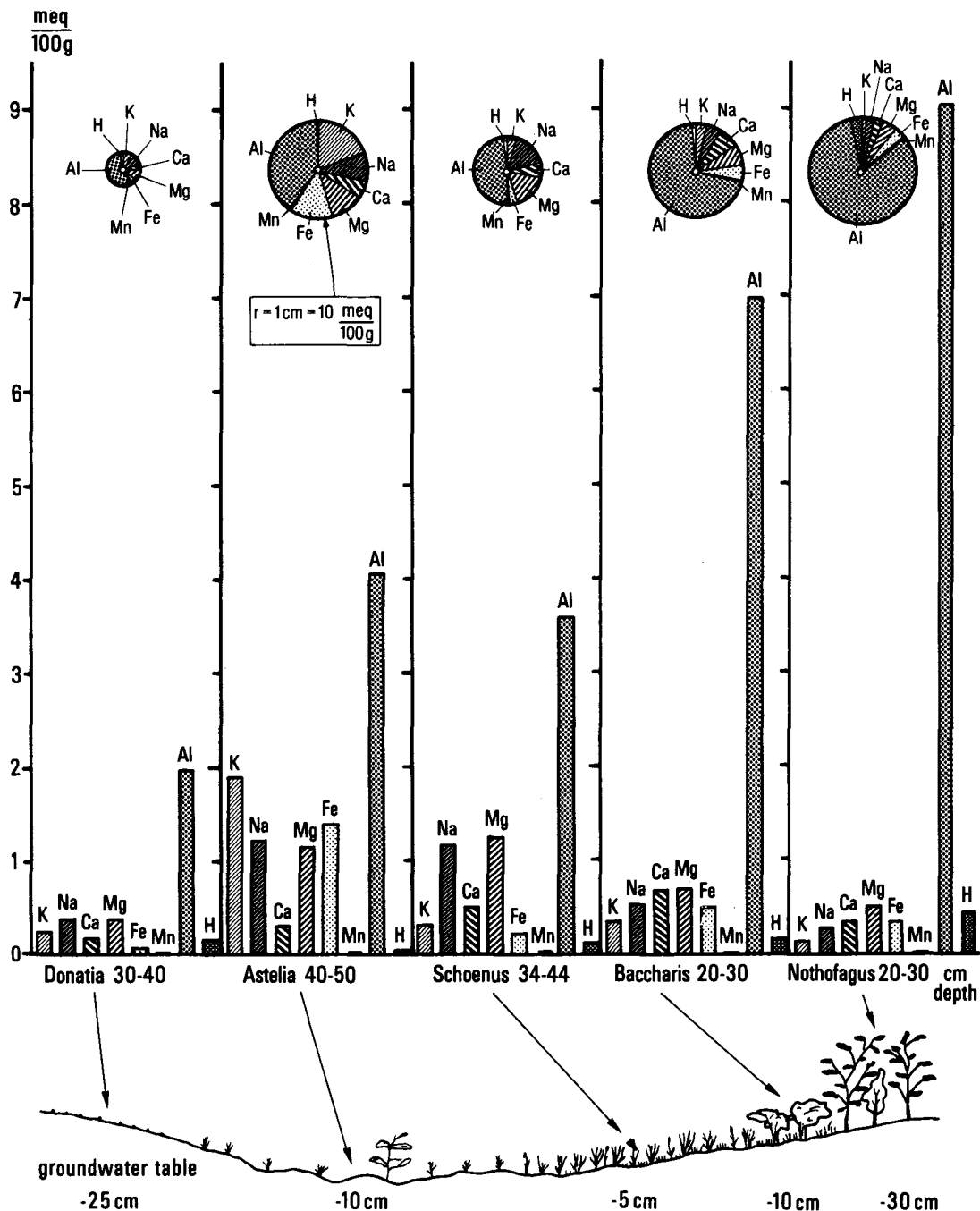
Exchangeable (NH_4Cl) cations (Pichihué)

Fig. 7: Contents of cations exchangeable with NH_4Cl from the lower layer of the soil profiles. Numbers in meq/100 g dry soil. The effective cation exchange capacity (CEC_{eff}) is presented in circle diagrams. Contenido de cationes intercambiables con NH_4Cl de la capa inferior de los perfiles de suelo. Valores en meq/100 g de suelo seco. La capacidad efectiva efectiva de intercambio de cationes (CEC_{eff}) está representada en diagramas circulares.

pected effect of the underground soil and/or groundwater. Free H^+ ions have a surprisingly small importance.

In the root layer of the soil (0-10 cm), the differences between the sites are greater and more varied (Fig. 8). Again, the increas-

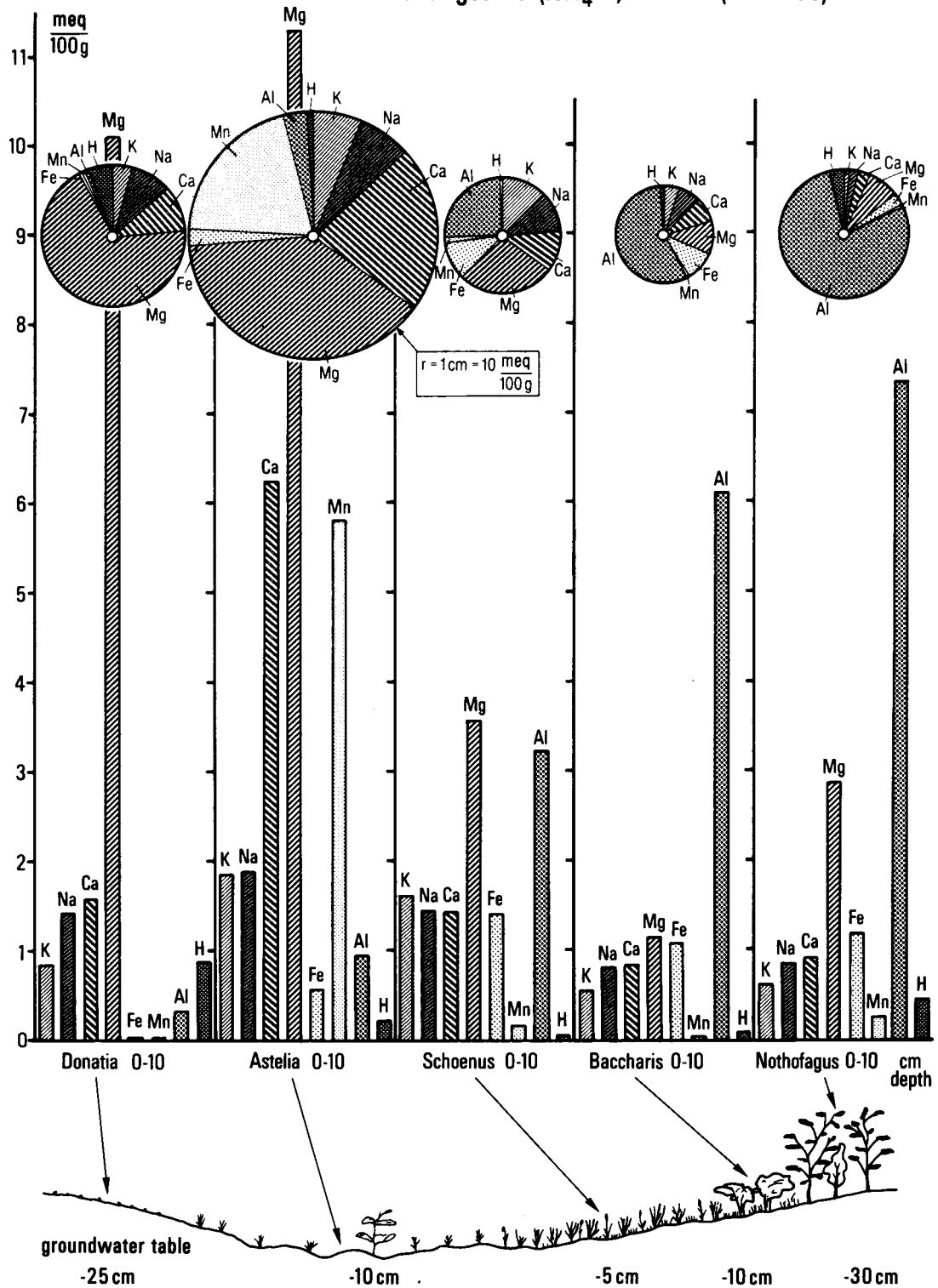
Exchangeable (NH_4Cl) cations (Pichihué)

Fig. 8: Contents of cations exchangeable with NH_4Cl from the upper layer of the soil profiles. Numbers in meq/100 g dry soil. The effective exchange capacity (CEC_{eff}) is presented in circle diagrams.

Contenido de cationes intercambiables con NH_4Cl de la capa superior de los perfiles de suelo. Valores en meq/100 g de suelo seco. La capacidad efectiva de intercambio de cationes (CEC_{eff}) está representada en diagramas circulares.

ing content of exchangeable Al represents the growing influence of the mineral soil from the center to the margin of the moorland. A similar trend occurs for Fe, which is present only in traces in the *Donatia* bog. Exchangeable amounts of Mn in the upper peat layer of the *Astelia* plot are very high (6 meq/100 g dry soil).

The supply of exchangeable Mg is relatively good in all plots, except in the *Baccharis* scrub. In the *Donatia* and the *Astelia* stands, the content of Mg is higher than 10-11 meq/100 g dry soil. The *Astelia* mire seems to have a better supply of Ca too than all the other sites. The portion of K and Na of the total CEC is lower than 1 meq/100 g dry soil with the exception of the *Astelia* and the *Schoenus* plot.

The plant-available amounts of potassium and phosphorus were also analyzed (Fig. 9). The availability of K is highest under the

Astelia carpet, still relatively good in the upper peat layer of the *Schoenus* fen, but much lower in the other moorland sites. The plant-available concentrations of P are very low in all soil samples analyzed (Fig. 10). Among them, the cushion-plant peat soils have the highest values. In all the other plots the concentrations of P are lower than 3 mg/100 g dry soil.

A general view of the nutrient supply of a site can be obtained on the basis of the total contents of the mineral plant nutrients in the soil.

In the lower soil layer (20-50 cm), the total contents of potassium and magnesium increased from the center to the border of the moorland (Table 2). This is due to the growing influence of the mineral soil and seepage water penetrating the peat soils. Al contents of the peat under the cushion-plant vegetation was 2-3 times

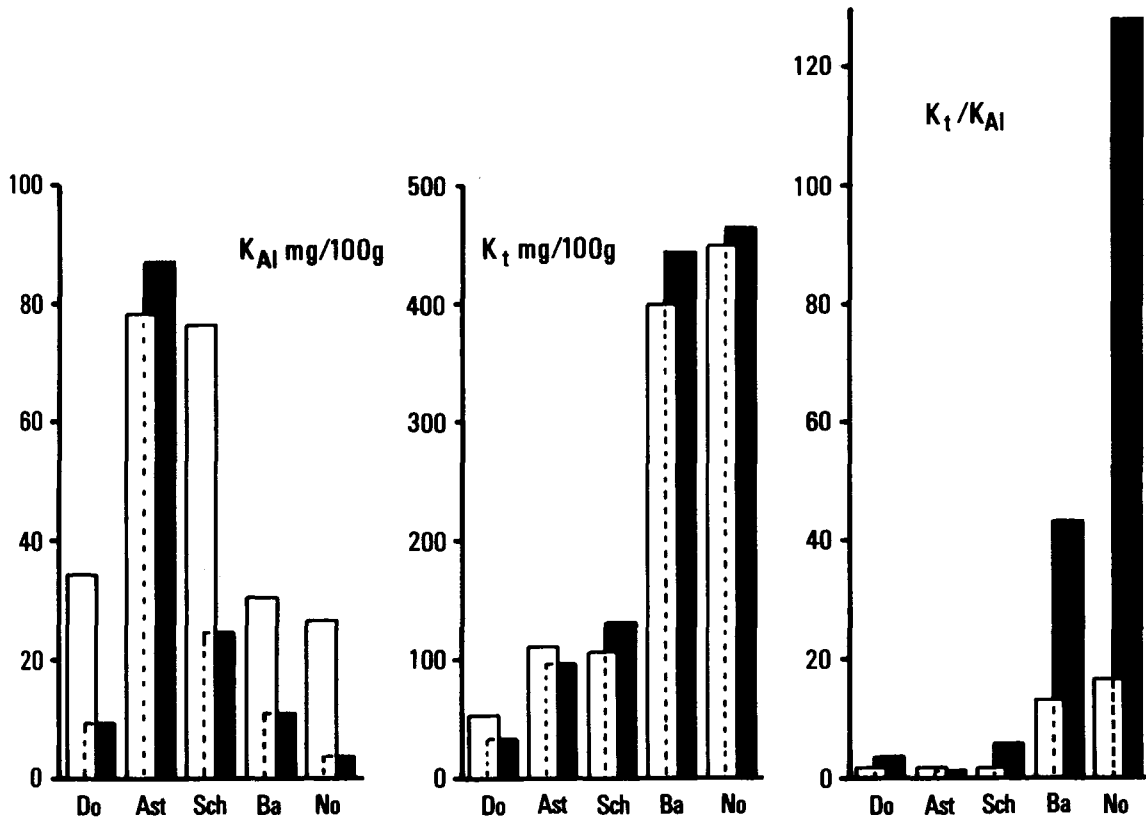


Fig. 9: Plant-available (extractable with NH_4 -lactate-acetic-acid) potassium (K_{AI}) and total contents of potassium (K_t) in the soils of typical moorland zones from the vegetation transect studied. Explanations see Fig. 6.

Contenido disponible para las plantas (intercambiable con lactato de NH_4 en ácido acético) de potasio (K_{AI}) y su contenido total (K_t) en los suelos de las zonas típicas de la transecta estudiada. Símbolos: vea Fig. 6.

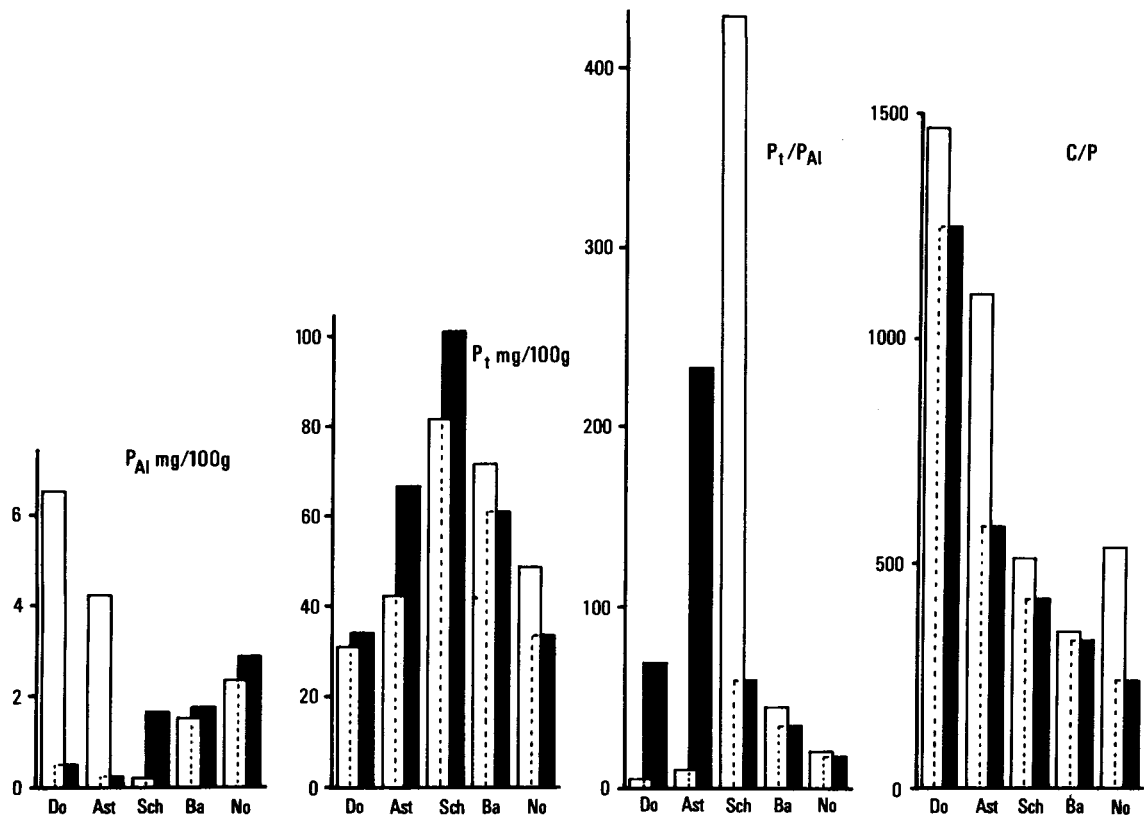


Fig. 10: Plant-available (extractable with NH_4 -lactate-acetic-acid) phosphorus (P_{Ai}) and total contents of phosphorus (P_t) in the soils of typical moorland zones from the vegetation transect studied. Explanations s. Fig. 6.

Contenido disponible para las plantas (intercambiable con lactato de NH_4 en ácido acético) de fósforo (P_{Ai}) y su contenido total (P_t) en los suelos de las zonas típicas de la transecta estudiada. Símbolos: vea Fig. 6.

lower than below the *Baccharis* scrub and the *Nothofagus* forest. The *Schoenus* fen, on the other hand, shows Al amounts of about 1.5 g/kg dry soil and has therefore the lowest Al concentration of all soils analyzed.

Total iron concentrations in the lower soil layer range from 6 g/kg dry soil below the *Schoenus* fen to 90 g/kg dry soil underneath the *Astelia* cushions. Studies of Damman (1978) show that some mineral elements are leached and concentrated in the layer affected by the regular changes of the water table. To these elements belong Fe, Al and Mn.

Na and Ca show similar trends. Their totals range from 0.2 to 0.8 g/kg dry soil and increase slightly from the center to the border of the moorland. Total Na and Ca in the lower soil layer of the *Notho-*

fagus forest are similar to the concentrations in the cushion-plant area. As the mineral soil has a higher bulk density, the content of an equal volume of soil should be higher in the mineral- than in the moor-gley.

The total amount of bases and acid-forming cations in the rooted soil layer (0-10 cm) reflects only partially the variation of its exchangeable fraction (Table 2). Al, and less markedly K, increased in the direction to the woodland. Fe concentrations are the highest below the *Schoenus*-fen in the center of the transect.

The mobile portions of Ca and Mn reflect their total contents in the soil. In the upper 10 cm peat soil, below the *Astelia* cushions, both are more concentrated than below the adjacent *Donatia* bog or *Schoenus* fen. Below the *Baccharis* scrub

TABLE 2

Total contents and plant-available (extractable with NH_4Cl) amounts of K, Na, Ca, Mg, Fe, Mn and Al as well as the effective cation exchange capacity (CEC_{eff}) of the soil profiles from typical moorland zones of the vegetation transect studied. Numbers in mg/kg dry soil

Contenido total y disponible para las plantas (intercambiable con NH_4Cl) de K, Na, Ca, Mg, Fe, Mn y Al seguido por la capacidad de intercambio de cationes (CEC_{eff}) de los perfiles de suelo en las zonas típicas de la transecta estudiada de turberas. Valores en mg/kg suelo seco

Soil character	cm	<i>Donatia</i> bog		<i>Astelia</i> mire		<i>Schoenus</i> fen		<i>Baccharis</i> scrub		<i>Nothofagus</i> woodland	
		0-10	30-40	0-10	40-50	01-10	34-44	0-10	20-30	0-10	20-30
t o t a l mg/kg	K _t	514	322	1,122	996	1,058	1,318	4,013	4,495	4,501	4,624
	Na _t	312	187	394	233	400	336	377	455	413	265
	Ca _t	1,066	284	4,895	254	976	497	826	842	724	336
	Mg _t	1,526	179	1,476	255	628	615	1,612	1,574	1,510	1,338
	Fe _t	671	10,442	4,411	96,379	38,408	5,821	21,330	14,541	8,087	7,789
	Mn _t	24	18	2,284	35	75	26	39	42	104	34
	Al _t	939	9,949	1,336	9,191	5,646	14,668	25,855	25,412	20,186	21,422
e x c h a n g e a b l e mg/kg	K	273	100	725	745	630	125	208	135	239	45
	Na	328	94	433	280	334	269	185	120	197	60
	Ca	317	40	1,249	63	289	100	164	135	182	66
	Mg	1,322	50	1,372	140	434	152	140	85	348	60
	Fe	8	29	157	387	390	63	300	135	354	89
	Mn	7	0.8	1,596	18	40	6	6	3	68	2
	Al	29	178	83	365	290	321	552	627	662	812
	H	8.7	1.8	2.1	0.4	0.5	1.2	0.9	1.5	4.6	3.9
meq/kg		158	35	288	102	129	72	106	99	146	110
CEC_{eff}											
pH (KCl)		2.9		3.6		3.8		3.6		3.2	
			3.5		3.8		3.6		3.5		3.1

and the *Nothofagus* forest, both elements have much lower total concentrations than below the *Astelia* carpet (Table 2).

The proportion of the exchangeable ions to their total contents is normally higher in peat than in mineral soils and in the upper than in the lower soil layers (Table 3). An exception again was the *Astelia* peat where values were the highest for all elements. For some of them (K, Na, Ca, Mn) there were no differences

between the upper and the lower soil layer.

Whereas the exchangeable portions of K and Mg in the mineral soil are quite low, because of their high total contents, the relative availability of Fe and Al was lowest in the peat soils.

To compare the total and plant-available K one can use the values for the fraction exchangeable with ammonium-lactate (Fig. 9). The result is the same: The mobile

TABLE 3

Relation between total and exchangeable (en NH_4Cl) amounts of K, Na, Ca, Mg, Fe, Mn and Al in the soil profiles from typical moorland zones of the vegetation transect studied

Proporción entre el contenido total y el intercambiable con NH_4Cl de K, Na, Ca, Mg, Fe, Mn and Al en los suelos de las zonas típicas de la transecta estudiada de turberas

Soil character depth cm	<i>Donatia</i> bog		<i>Astelia</i> mire		<i>Schoenus</i> fen		<i>Baccharis</i> scrub		<i>Nothofagus</i> woodland	
	0-10	30-40	0-10	40-50	01-10	34-44	0-10	20-30	0-10	20-30
K_t/K	1.8	3.0	1.5	1.3	1.8	10.4	19.2	33.3	18.8	104
Na_t/Na	1.0	2.0	0.9	0.8	1.2	1.3	2.0	3.8	2.1	4.4
Ca_t/Ca	3.4	7.1	3.9	4.0	3.4	5.0	5.0	6.2	4.0	5.1
Mg_t/Mg	1.2	3.6	1.1	1.8	1.5	4.1	11.5	18.5	4.3	22.3
Fe_t/Fe	84	360	28	249	98	92	71	108	23	88
Mn_t/Mn	3.4	22.5	1.4	1.9	1.9	4.3	6.5	14	1.5	17
Al_t/Al	32	56	16	25	20	46	47	23	31	26

fractions in the soil are 40 to more than 100 times smaller in the mineral soils.

Because phosphorus is a critical factor in mire ecosystems, it was analyzed in all soils (Fig. 10). Its total content is highest where its available fraction is lowest. Values are lowest in the upper soil layer of the *Schoenus* fen, and highest in the cushion bogs and the *Nothofagus* forest.

In the lower peat layer of the *Donatia* and *Astelia* mires P is hardly mobile. This is clearly shown by the $\text{P}_t/\text{P}_{\text{Al}}$ ratios (Fig. 10). They are related to the Fe fraction of the same soil layers. High Fe concentrations, as found in the upper layer of the *Schoenus*-fen and the lower layer of the *Donatia* and *Astelia* peat, may fix the generally low contents of P when FeIII-hydroxy-ions are present. In a reducing environment Fe is present as FeII, which cannot combine with P in the same way.

The small mineralization rate of P in the peat soils can be deduced also from the extremely large C/P ratios (Fig. 10). C/P ratios decreased from the center to the

margin of the moorland, at the same time that P-mineralization rate increased.

DISCUSSION

The effect of mineral nutrition on vegetation pattern

It is difficult to draw definitive conclusions about the effects of the nutrient supply on the moorland zonation on the Cordillera de Piuchué. Some suggestions discussed here, are based additionally, on yet unpublished studies of other two transects.

It can be proposed that the Al, Fe and Mn in the soils have their origin in the weathering processes of the underlying schists. The contents of K, Ca and Mg may be enriched by deposition of salt spray coming from the Pacific coast to the west. Because Na is relatively mobile it should be leached quickly under high precipitation. Similar leaching processes are likely for the other bases, where the vegetation

cannot retain them effectively. The input of oceanic salts should increase from the center to the border of the moorland, as the roughness of the surface increases, and therefore the retention of particles and aerosols from clouds and fog in the forested slopes raises as well.

Nearly all mineral nutrients should be fairly mobile because the soils are continuously wet and have reducing conditions associated with extremely low pH-values. The high annual precipitation (over 3,000 mm) should enhance all leaching processes, even on slightly inclined slopes.

The area chosen for the present investigations has small, but important topographic differences. The *Astelia* carpet covers the lowest point of the transect. The area rises slightly to both sides. The gradient is more pronounced in the direction of the *Donatia* bog than to the opposite side, where the moor ends at the base of a steeper slope covered by *Nothofagus* forest. There are underground water pathways leading from the *Donatia* bog and from the mountain slope to the depression covered by the *Astelia* carpet.

On the other hand, there is a slight southwest slope and the depression is drained in this direction by a small stream. Probably, both the *Schoenus* fen and especially the *Astelia* mire receive additional water with dissolved mineral compounds from the small drainage basin. Thus the *Astelia* community should receive more water with dissolved minerals than all the other moorland types, especially when snow melts or during heavy rains.

The *Nothofagus* forest grows on a steep slope. It might receive a somewhat higher precipitation than the open moorland. The water draining from this slope passes through the *Baccharis* scrub and eventually reaches slowly the *Schoenus* fen.

In this contact zone, we find plants such as *Carex magellanica*, *Carpina alpina*, *Carex canescens*, *Pratia repens*, which are absent from the rest of the transect. The soil is wetter here than in the *Schoenus* fen zone. *Carex magellanica* and *Carex canescens* occur also in the northern hemisphere. In Europe they indicate transitional sites between raised bogs and fen vegeta-

tion. They are frequent also in the margin of raised bogs, where drainage water from the contiguous slopes accumulates. This may be true to some extent for the transect studied.

Because nutrient concentrations are given per soil weight, they can only be used for comparisons within the group of the peat soils (*Donatia*, *Astelia*, *Schoenus* formation) or within the more mineral soils (*Baccharis* scrub, *Nothofagus* forest).

The development of *Astelia* cushions will be favored by continuous flow of water bringing a steady mineral supply. Whereas Fe and Al will be highly immobilized. Ca, Mg and Mn are bound in a reversible form to the soil surface and remain available for the plants. K and Na seem to be either available in small quantities (K) or easily leachable (Na). The *Astelia* formation occupies the site with the best nutrient supply of all the vegetation types investigated. This may be reflected in the rapid growth of *Astelia* cushions and the fact that small *Nothofagus antarctica* trees are found there.

Compared to *Astelia* cushions, the *Donatia* bog is lower in K and Ca, but has similar amounts of Mg. In the lower peat layer of the *Donatia* bog contents of all nutrients are lower than below the *Astelia* cushions. The low exchangeable rates of Fe, Mn and Al are striking and relevant for the vegetation pattern. The concentrations are too low to produce toxic effects. Rather, plants growing here should be adapted to survive on sites with a poor provision of these elements. Their low availability contrasts with the high total concentration of the immobile fractions of Fe and Al. However dried soil samples may have caused irreversible changes in the exchange conditions of the peat.

Schoenus fen has a lower Mg supply than the *Donatia* bog. Exchangeable Fe and Al are often higher than in the soils of the cushion-plant formations. This may be related to the permanently high water table and the continuous influence of seepage water from the bordering mineral soils. The *Schoenus* community has several characteristics of a poor sedge lawn in northern Europe.

A similar analysis of the availability of nutrients (Na, K, Ca, Mg) in the upper peat layer (5-15 cm depth) of analogous plant formations was performed by Smith (1981) in a moorland of South Georgia. The pH-values of the comparable *Cyperaceae*-moorland ranged from 4.0 to 4.8 and were related to the stagnant or seeping ground water regime. The humus content was much lower (C_t : 1-3%) than in the moorland of Chiloé. Na and K concentrations (soluble in NH_4Cl -extracts) of the upper soil layer were in the same range as in the cushion bogs and sedge lawns on the Cordillera de Piuchué. The availability of Ca was 10 times higher in the moorland of South Georgia. The lower limit of these values compare to the Ca-availability in the upper peat of the *Astelia* plot. The Mg supply, in contrast, seems to be higher in Chiloé.

The *Baccharis* scrub resembles the *Nothofagus* forest in its mineral nutrition. With the exception of Mg, values are higher than in the open moorland. The supply of bases should be even higher because plant roots may reach the mineral soil.

The total moorland complex probably, suffers from P deficiency, which is most pronounced at the *Schoenus* site.

Combining field observations with the results of the chemical analysis of soils we suggest that the vegetation responds to the different nutrient conditions and that the vegetation pattern of the moorland reflects differences in topography and drainage.

Only the *Donatia* community occurs under similar conditions to raised bogs in Europe or North America and might be called a *Donatia* "bog", because of its extremely poor mineral supply. All other formations show more correspondence with sites of "fen" vegetation and poor moist woodland ("Bruchwald").

Transition between woodland and open moorland

The Magellanic moorland grows in contact with evergreen subantarctic woodlands throughout its geographical range in southern Chile. To understand its particular

characteristics, one should look for the reasons why trees cannot colonize the moorland. In addition to natural causes, anthropogenic factors may play a role in explaining the transition between woodland and moorland.

The natural growth and strength of the trees could be impaired by water saturating the root soil layers and by the depression of leaf temperatures due to wind exposure (Fig. 3). The water saturation of soil has complex effects on the availability of nutrients and toxic elements, and the ability of the roots to uptake nutrients. The deficient supply of oxygen in water logged soils inhibits all root activities.

The common appearance of stunted trees showing branching in an eastern direction on the Cordillera de Piuchué is caused by the predominant westerly winds. The effect of wind is reinforced by the transport of ice needles in winter or salt spray from the ocean. These effects are especially visible in the *Fitzroya* trees, which dominate on the upper western slopes. Isolated individuals of *Nothofagus betuloides* and *N. nitida* growing on the open moorland are also affected by wind (Fig. 3).

In the last decades, human use of the vegetation of the mountain range of Chiloé has increased. *Fitzroya* trees have been debarked to use the bark for sealing wooden boats and ships. The loss of its bark may weaken and eventually kill the trees. The thick layer of epiphytes may also protect the tree against frost and drought or even fire. The dense cover of epiphytes around its trunks is formed by mosses interlaced with lianas (*Philesia magellanica*) and the rhizomes of ferns (*Hymenophyllum* spp.). This thick moss cover may serve as filter for precipitation inputs in this forest ecosystem. The loss of the epiphytes alters the storage of nutrients to prevent leaching in the soil compartment.

When shrubs or trees are weakened or decay, moorland plants can replace them. These species possess several characters which favor their growth on wet and nutrient poor sites. It was observed that in various places moorland species like *Schoe-*

nus antarcticus, *Oreobolus obtusangulus*, *Astelia pumila* and *Donatia fascicularis* invade forest sites disturbed by fire several years before (Fig. 11). *Astelia* can cover rapidly fallen trunks and the base of standing dead trees.

The understory of poorly growing, relatively open woodlands of *Fitzroya*, *Pilgerodendron* and *Nothofagus nitida* are sometimes colonized by moorland species. If moorland plants succeed in forming a continuous carpet, the establishment of tree seedlings may be seriously impaired.

The extreme microclimate of the open moorland may be an additional complication for tree growth. The *Donatia* bog may dry up during dry summers. In winter, frost can penetrate the upper peat layer. Periods with frost during the nights and high temperatures during the day can produce frostheaving and destruction of the closed cushion plant carpet. Small holes or depressions can be formed and filled with rain water. On slopes, moorland terraces have evolved due to solifluction movements. Similar observations have been made by Roig *et al.* (1985) in Patagonia.

Longer-term climatic changes may control the local distribution pattern of the woodland and moorland, especially changes in the precipitation regime. Increasing rainfall, shortened dry periods and reduced radiation would favor the extension of

the moorland and viceversa. Decreasing temperatures in combination with more continental climate could perhaps damage the cushion plants, because of the frost. In this case the continuously wet sedge fen areas would be less damaged, because they will hardly freeze to a great depth.

Considerations about succession

The present pattern of the open moorland on the Cordillera de Piuchué seems to be in agreement with the present ecological conditions. Only in areas where the forest has been disturbed or roads have been built, successional processes are taking place.

The differences in the water and nutrient relations are sufficient to explain the variation in the vegetation pattern. Results of the pollen analysis for this area (Villagrán 1988, 1991) show at 80 to 100 cm depth high portions of *Astelia* and *Donatia* pollen as well as of other moorland species. At the beginning of the profile *Astelia* shows a peak followed by a *Donatia* peak. After, *Gaimardia* has a low but constant amount of pollen. It is possible that this pattern represents a successional sequence associated with increasing precipitation.

Greater portions of *Astelia* pollen appear only in the lowest layer of the peat core indicating the initial stages of an open moorland. This species is present in the profile until today, but with small values. Pollen of *Donatia* disappears several times from the peat samples, but increases in the uppermost centimeter.

These changes can be a consequence of recent human destruction of the forests. Similar results have been discussed by Godley & Moar (1973) based on a peat core from the Cordillera de San Pedro in Chiloé. In their sample core, pollen of *Tapeinia* increases in the upper peat layer. In both cases a *Nothofagus* forest is present in the surroundings of the bog and determines the pollen composition of the peat in a decisive way.

Schoenus antarcticus is more frequent on the slopes surrounding the *Donatia* bog than in the central area. *Schoenus* could decrease when the precipitation is increasing. Lough *et al.* (1987) have describ-



Fig. 11: Cushion-plant moorland on the western slope of the Cordillera de Piuchué/Chiloé at about 600 m, surrounded by *Fitzroya-Nothofagus* woodland damaged by fire.

Turbera de plantas en cojín en la ladera occidental de la Cordillera de Piuchué/Chiloé en alrededor de 600 m, rodeado de un bosque de *Fitzroya* y *Nothofagus* destruido por fuego.

ed a similar situation in the mountains of New Zealand, where sedges compete with cushion-plants. The very humid sites of the *Schoenus* fen are influenced by additional seepage water and maintain less peat. In these places, an extense carpet of *Sphagnum magellanicum* covers the ground. In Europe this species grows predominantly on ombrotrophic bogs. In Chiloé and other parts of southern Chile (Pisano 1977) *Sphagnum* seems to be less tolerant of extremely poor mineral nutrition.

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