ACTA BOTANICA GALLICA

BULLETIN DE LA SOCIETE BOTANIQUE DE FRANCE
Parution trimestrielle

VOLUME 151 (1), **mars 2004**

TABLE DES MATIÈRES

Les sommaires d'*Acta botanica Gallica* sont reproduits dans les *Currents Contents*, indexés dans les différentes publications de l'*Institute of Scientific Informations* (Philadelphie, U.S.A.), dans les Abstracts et Index de *Bioscience Information* Service of Biological Abstracts (Philadelphie, U.S.A.), dans le *BioPascal-Folio* du C.N.R.S. (Paris), ainsi que dans *Geo Abstracts* et *Geobase*.

CONTENTS

*Acta Bot. Gallica, 2004, **151** (1), 3-31.*

The *Nothofagus nitida* (Phil.) Krasser woodlands of southern Chile in the northern half of their range: phytosociological position

by Javier Amigo([1]), Carlos Ramírez([2]) and Luis G. Quintanilla([3])

(1) Laboratorio de Botánica, Facultad de Farmacia, Universidad de Santiago de Compostela, E-15782 Santiago de Compostela, Galicia. E-mail: bvherbar@usc.es

(2) Instituto de Botánica, Universidad Austral de Chile, Casilla 567, Valdivia, Chile

(3) Departamento de Ciencias experimentales e Ingeniería, Universidad Rey Juan Carlos, C/ Tulipán s/n, E-28933 Móstoles, Madrid

arrivé le 18 juin 2003, accepté le 24 septembre 2003

Abstract.- A phytosociological study of the temperate rain forests dominated by an evergreen species endemic to Chile, one of the highest-rainfall woodland types of temperate South America, included within the geobotanical concept of North Patagonian Forest. Relevés were taken from throughout an area comprised between 40° and 44° 40' South, in which these woodlands show highest floristic richness. The community's floristic and structural diversity are described and proposed as an independent association, *Luzuriago polyphyllae-Nothofagetum nitidae* ass. nova. The ultrahyperhumid character of this association is evidenced by the number of Hymenophyllaceae species (filmy ferns) that may occur within it.

Key words : syntaxonomy - temperate rainforest - Patagonian forest - structure - Hymenophyllaceae.

Résumé.- Cette étude phytosociologique porte sur les forêts humides tempérées dominées par une espèce à feuilles persistantes endémique du Chili, un type de forêt nord-patagon du point de vue géobotanique et une des plus arrosées de toute l'Amérique du Sud tempérée. Nous avons rassemblé des relevés tout au long du territoire compris entre les parallèles 40° et 44° 40' Sud, là où ce type de forêt trouve son optimum floristique. Après la description de ses composition floristique et diversité structurale, nous affirmons son originalité syntaxonomique sous le nom de *Luzuriago polyphyllae-Nothofagetum nitidae* ass. nova. Son caractère ultrahyperhumide est marqué par une diversité d'espèces d'Hymenophyllaceae.

Mots clés : syntaxonomie - forêt pluviale temperée - forêt patagone - structure - Hymenophyllaceae.

I. INTRODUCTION

Nothofagus nitida (Phil.) Krasser is a broad-leaved evergreen tree species endemic to Chile. Its area of distribution extends from 39° 53' to 48° 30' S (Ormazábal & Benoit, 1987), in the 10th and 11th regions (following the official nomenclature dividing Chile into 13 regions; see for example Marticorena & Rodríguez, 1995). Its local name, coihue de Chiloé, reflects its broad-leaved character, shared with two other Chilean species, *Nothofagus dombeyi* (coihue), the most widely distributed of the three, extending from 34° 31' to 48° S, and *Nothofagus betuloides* (coihue de Magallanes), which extends from 40° S to the southernmost extreme of Tierra de Fuego, practically 56° S. The distribution of *Nothofagus nitida* coincides precisely with the latitudinal belt in which the ranges of the other two coihues overlap (Ormazabal & Benoit, 1987), and of the three species it is the least tolerant of continentality. In other words, of the oceanic coihues it is that which occurs at lowest altitudes (McQueen, 1976) and thus the only one not found in Argentina. This biogeographical behaviour may be related to a more ancestral phylogenetic position than *N. dombeyi* and *N. betuloides*, as argued by Premoli (1996) on the basis of leaf architecture and alloenzyme studies.

Nothofagus nitida reaches heights of 35 to 40 m, and thus may be a dominant component of the canopy layer, although it generally shares dominance with other broad-leaved and/or coniferous species. Woodlands in which *Nothofagus nitida* is present were included in classical phytosociological classifications as "Valdivian woodland" or "Valdivian rainforest" (Reiche, 1907; Skottsberg, 1910; Hauman, 1913), since for these authors the Valdivian territory extends from between 38° and 41° S to between 46° and 48° S. However, later geobotanical studies such as Schmithüsen (1956) and Oberdorfer (1960) indicate a subdivision of the wet temperate woodlands of southern Chile into three belts, not two, denominated Valdivian, North Patagonian and Magellanic; this scheme offered a better account of the gradual north-to-south decline in floristic richness in these woodlands extending over almost 18° of latitude. More recently Ramírez and Figueroa (1985), who used a multivariate analysis approach, placed the *Nothofagus nitida* woodland clearly outside the group defined as "Valdivian".

In subsequent non-phytosociological studies that have proposed classificatory schemes for the Chilean temperate woodlands, authors have differed as to whether they recognize a category of woodland dominated by *Nothofagus nitida*.

Firstly, Veblen and Schlegel (1982) divided the woodlands of southern Chile into 23 types (3 deciduous and 20 predominantly evergreen, including coniferous). For the first time they established a forest type that was denominated "*Nothofagus nitida - Saxegothaea - Podocarpus nubigenus* [sic] - *Weinmannia*", in which *Nothofagus nitida* is recognized as dominant and which these authors consider to extend along the Coastal Range from southern Valdivia to Chiloé island. The classification also includes a type denominated "Evergreen *Nothofagus - Weinmannia*", which extends along the coastal belt, further south than the *Nothofagus nitida* type, and in which all three *Nothofagus* species may occur.

Secondly, Gajardo (1994) likewise presents a descriptive summary and additionally provide a cartographic representation of the vegetation units recognized throughout Chile. This author names one of his cartographic units "bosque laurifolio de Chiloé" [Chiloé laurifoliar woodland], within which he recognizes two "type communities" dominated by *Nothofagus nitida*; these type communities are designated by the name of the dominant species and by another species frequently occurring, thus *Nothofagus nitida-Podocarpus nubigena* and *Nothofagus nitida-Tepualia stipularis*.

Thirdly and finally, the classification most widely used by the Chilean administration and in the academic community has been the Forest Types classification of Donoso (1981). According to this classification, *Nothofagus nitida* may occur in woodlands of various types, mostly within the Evergreen forest type, but also in the Alerce, Guaitecas Cypress and Magallanes Coihue types.

The study of Oberdorfer (1960) offers the precision of phytosociological systematics, grouping the wet temperate communities of Chile into the phytosociological class *Wintero-Nothofagetea*, and within this class designating the alliance *Nothofago-Winterion* to include the "North Patagonian laurifoliar woodlands"; however, this basic work of Chilean syntaxonomy does not include a specific phytosociological unit corresponding to *Nothofagus nitida* woodlands. Within *Nothofago-Winterion* Oberdorfer considers only three associations dominated by broad-leaved species: tepa-tineo woodland (*Laurelio philippianae-Weinmannietum trichospermae*), pure North Andean coihue woodland (*Chrysosplenio valdivici-Nothofagetum dombeyi*) and pure Magallanes coihue woodland (*Nothofagetum betuloidis*), though this latter is placed in a separate suballiance. Also assigned to *Nothofago-Winterion* by Oberdorfer were two conifer-dominated associations, *Fitzroyetum cupressoidis* and *Pilgerodendronetum uviferi*. In this scheme, *Nothofagus nitida* occurs only in the relevés of *Nothofagetum betuloidis* and *Pilgerodendronetum uviferi*. Oberdorfer's work is of course of great value, but in this particular case his interpretation perhaps reflects a lack of fieldwork to the south of the Lakes Region; in fact *Nothofagetum betuloidis* was described by this author, but on the basis of relevés compiled from previous studies such as Reiche (1907) and Skottsberg (1916).

Subsequently, Chilean authors using phytosociological methods have delimited a community denominated "*Nothofagetum nitidae*" (Ramírez & Figueroa, 1985); although they did not publish their relevés, they did present tabular data on species presences, in order to classify woodland associations with the aim of defining the concept of Valdivian woodland. It was inferred that this *Nothofagetum nitidae* shows more affinity with *Chrysosplenio-Nothofagetum dombeyi, Fitzroyetum cupressoidis* and *Pilgerodendronetum uviferi*, and this group (denominated Chiloé woodland, Bosque chilote) is classed as "cold humid" in contraposition to the Valdivian woodland group classed as "temperate humid".

Ramírez and Figueroa (1987) likewise do not present relevés, in a study which aims to offer a summary of the phytosociological behaviour of the different species of the genus *Nothofagus* in the Chilean hygromorphic zone (following the phytogeographic terminology of Fuenzalida & Pisano, 1965). Although these authors reiterate the idea of a *Nothofagetum nitidae*, optimally developed in mainland and insular Chiloé, this name remains a nomen nudum.

There has thus been considerable diversity of opinion as regards the discrete existence of a woodland type dominated by *Nothofagus nitida*. The present study argues for the existence of such a woodland type as phytosociological association, and documents its biogeographic position, principal ecological and structural characteristics, differentiation from other communities, variability within geographical range, and syntaxonomic position.

II. STUDY AREA

The entire range in which *Nothofagus nitida* occurs falls within the Sub-Antarctic Province of the Antarctic Region (biogeographic classification of Cabrera & Willink, 1973). The range largely corresponds to the Valdivian District and the northernmost part of the Magellanic District as defined by these authors (i.e. boundary at the 47th parallel). In terms of more recent biogeographical proposals, the range of *Nothofagus nitida* lies within the Valdivian Province of the Valdivian-Magellanic region (Rivas-Martínez & Penas, 1994).

The territory sampled for the present study extends from the 40th parallel (the northernmost limit of the range of *Nothofagus nitida*, in the Valdivia National Reserve, just to the south of the city of that name) to 44° 40' S (the latitude of Puerto Cisnes in the foothills of the Andes; Fig. 1). This is thus only the northern half of the range of this species, but certainly the richest and most floristically diverse, for evident bioclimatic reasons. In an analysis of patterns of floristic richness in the temperate rainforests of South America between the 38th and 55th parallel, Arroyo *et al.* (1996) found that species richness (both for trees and for lianas and ferns) was maximal between the 40th and 44th parallels.

A. Physiographic units

The study area includes the principal physiographic elements of south-central Chile: the Coastal Range in the west and the Andean Range in the east. The zone corresponding to the Central Valley, a depression located between these two ranges, has practically no *Nothofagus nitida*. In the present study we thus distinguish three main physiographic zones with woodland containing this species:

Zone A: The Coastal Range from south of the city of Valdivia to the Piuchué Range (isla Grande de Chiloé, hereinafter Chiloé island), in which these woodlands are located at rather high altitudes, between 700 and 900 m. As shown in Fig. 1, *Nothofagus nitida* is present throughout Chiloé island, but due to the major anthropic impacts at lower altitudes on this island, we include in this category only relevés for acceptably natural *Nothofagus nitida* formations from the higher-altitude sites in the Piuchué Range.

Zone B: A zone that we designate "Piedemontes", including both the Andean foothills (generally of low altitude, not far from the sea, throughout the provinces of Llanquihue, Palena and Aysén, and including a sample from the Puyehue National Park) and the lower-altitude areas of Chiloé Island (specifically, relevés of the hygrophilous variant with *Tepualia stipularis*, from the foothills of the Piuchué Range, close to sea level but still within the Chiloé National Park). In this zone *Nothofagus nitida* woodlands are predominant at lower altitudes (*i.e.* the lower slopes of the Andes); we have also included in this zone relevés from higher-altitude areas, such as the Puyehue National Park (the most northeasterly of the relevés).

Zone C: The Aysén islands and Channels zone, comprising the fragmented territory of islands and peninsulas from the Guaitecas archipelago (sampling station n° 4 in Fig. 1) and further South. Our references to this third zone will be based on literature review only: it is in any case well known that *Nothofagus nitida* occurs in the dominant woodland communities of this territory (see Gajardo 1994).

B. Climate

These three physiographic zones cover a large territory (9° latitude), but all show two climatic features that can be considered characteristic of *Nothofagus nitida* woodland: high oceanicity and very high rainfall (Fig. 2). Mean temperatures range from 12.2 °C in

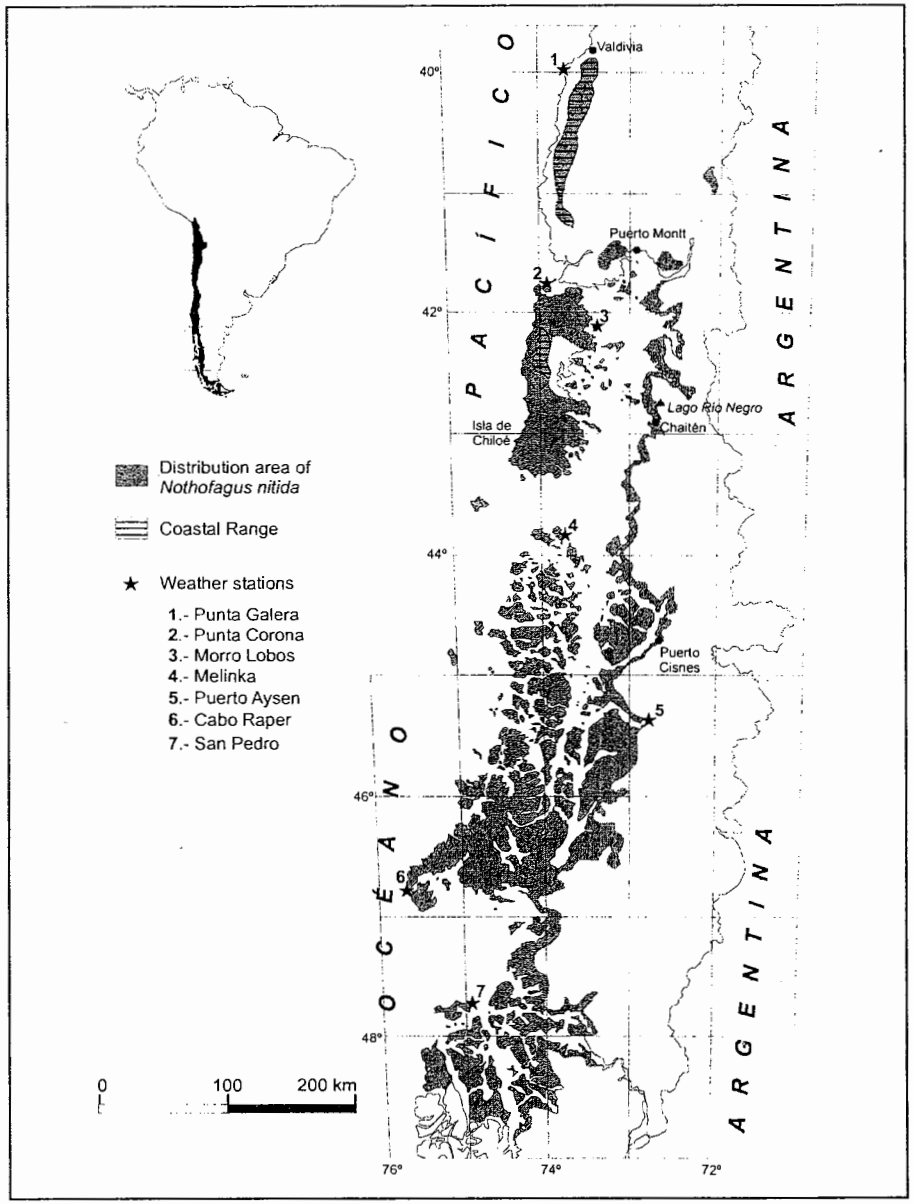
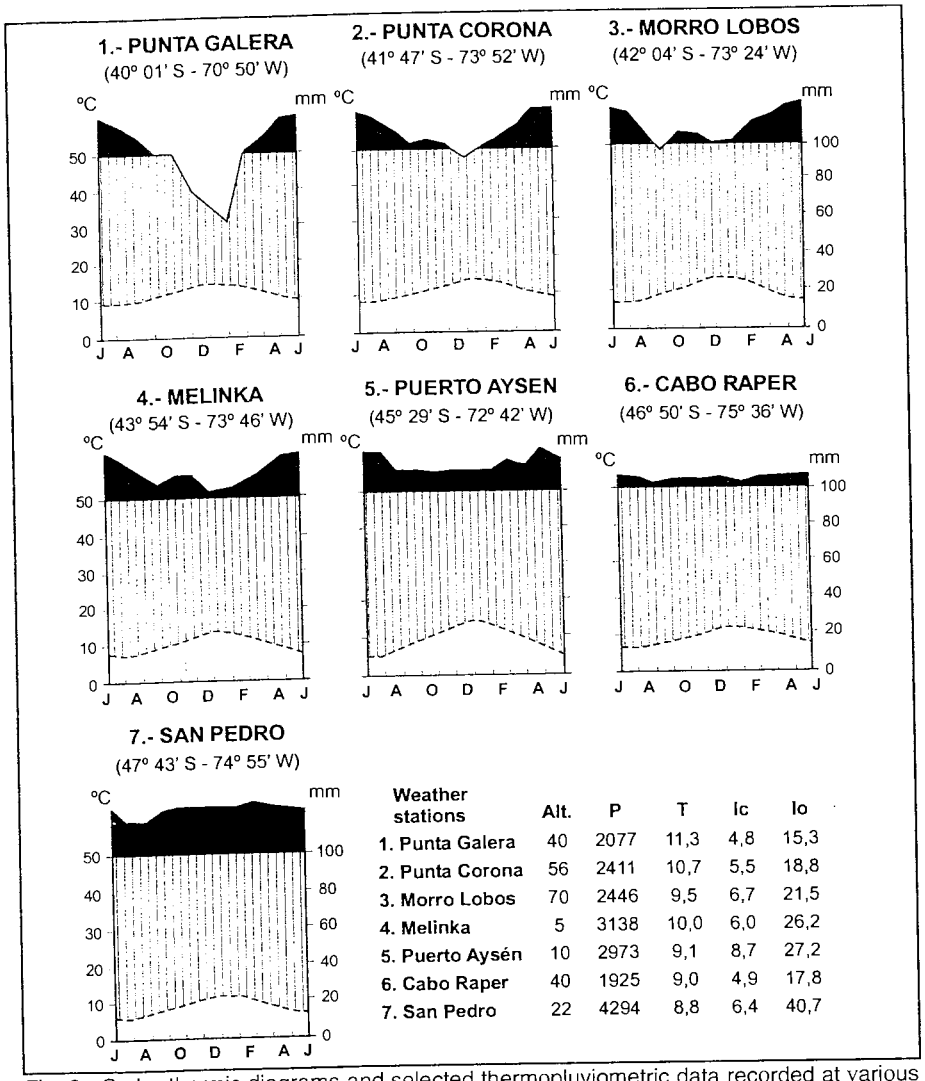


Fig. 1.- Map showing the distribution of *Nothofagus nitida*, based on CONAF (1998) and modified with own data. Points 1-7 are the weather stations listed in Fig. 2.

Fig.- 1.- Carte montrant la distribution de *Nothofagus nitida* suivant CONAF (1998) modifiée avec notres propres données. Les points numérotés de 1 à 7 représentent la localisation des stations météorologiques rapportées à la Fig. 2.



Weather stations	Alt.	P	T	Ic	Io
1. Punta Galera	40	2077	11,3	4,8	15,3
2. Punta Corona	56	2411	10,7	5,5	18,8
3. Morro Lobos	70	2446	9,5	6,7	21,5
4. Melinka	5	3138	10,0	6,0	26,2
5. Puerto Aysén	10	2973	9,1	8,7	27,2
6. Cabo Raper	40	1925	9,0	4,9	17,8
7. San Pedro	22	4294	8,8	6,4	40,7

Fig. 2.- Ombrothermic diagrams and selected thermopluviometric data recorded at various stations with the range of *Nothofagus nitida*. Alt. = altitude in m. a.s.l; P = mean annual precipitation; T = mean annual temperature; Ic = index of continentality (difference between the daily mean temperatures of the hottest month and the coldest month); Io = ombrothermic index [calculated as: Io = 10 (Pp/Tp), where Pp and Tp are the sums of mean monthly P and T, but months in which mean temperature is less than 0 °C are not taken into account]

Fig. 2.- Diagrammes ombrothermiques et données thermopluviométriques des différentes stations météorologiques situées dans l'aire de distribution de *Nothofagus nitida*. Alt. = altitude en m ; P = précipitation moyenne annuelle ; T = température moyenne annuelle ; Ic = indice de continentalité (différence entre les températures moyennes du mois le plus chaud et du mois le plus froid) ; Io = indice ombrothermique [calculé par la formule Io = 10 (Pp/Tp), où Pp et Tp représentent les sommes des valeurs moyennes mensuelles de P et T en excluant les valeurs correspondents aux mois où T < 0 °C].

Valdivia (39° 48' S) to 7.1 °C in Puerto Edén (49° 08' S), with thermal amplitude (*i.e.* difference between the mean temperatures of the coldest and hottest months) not exceeding 9.5 °C (Amigo & Ramírez 1998), though it should be noted that almost all of the weather stations within our study area are located below 100 m altitude.

Perhaps more relevant are the precipitation totals recorded in all these stations: most reach 2000 mm p.a., and at sea level greatly exceed this amount. Both in zone B (Piedemontes) and zone C (Aysén islands and Channels) there are several weather stations with rainfall between 4000 and 5700 mm (MOP, 1987). But even in the northernmost part of zone A (*i.e.* the area known as the Pelada Range, which has been studied in detail by one of us as regards vegetation diversity along an east-west transect; Ramírez *et al.*, 1996), annual rainfall is more than 4000 mm (Ramírez & Riveros, 1975). Indeed it was in the Pelada Range that Weinberger (1973) performed a study of variation in summer rainfall between different altitudinal belts: in the altitudinal belt in which *Nothofagus nitida* occurs summer rainfall was between about 500 mm on the slope above the Central Valley and 900 mm on the western slope. Another study in this area recorded rainfall over a one-year period only (Guitiérrez, 1984), and comparison of these rainfall data with simultaneous data for similar altitudes and latitudes in the Andean Range led Donoso *et al.* (1990) to talk of a "Mediterranean influence" in the Pelada Range; in our view, however, this is perhaps an exaggeration.

The combination of high rainfall and mild temperatures recorded at the weather stations in the study area lead us to classify these *Nothofagus nitida* woodlands as optimally ultra-hyperhumid, in the sense proposed by Rivas-Martínez (1995); an updated listing of the threshold values for the different ombrotypes included in this classification, based on calculation of the ombrothermic index (*Io*), is included in Rivas-Martínez and Loidi (1999). Additionally, *Nothofagus nitida* woodlands may also occur in hyperhumid areas ($12 < Io < 24$), but in such cases *Nothofagus nitida* tends to seek edaphic compensation and associates with *Tepualia stipularis* in characteristic hygrophilous formations (discussed below).

C. Soils

In zone A, the Coastal Range is the area with the oldest geological substrates, at least Paleozoic and in some cases Precambrian, and is the only part of our study area that was not covered by the Pleistocene glaciations (Villagrán *et al.*, 1996). The predominant rocks here are phyllites, quartzites, schists and mica schists, from which even red clay soils may be derived. But in the altitudinal belt in which *Nothofagus nitida* is found, soils are characteristically yellowish brown on well-drained slopes, becoming podsols closer to the hill-top and in flatter areas (Peralta, 1975). Clearly podsolic soils with deficient drainage in flat hill-top sites are an ideal position for the *Fitzroya cupressoides* woodlands ("alerzales"), which may occur in mosaic with patches of *Nothofagus nitida* woodland (Lusk, 1999). This vegetation is seen for example in the Coastal Range around the latitude of Osorno, where altitude scarcely exceeds 800 m and where there is no clear altitudinal separation of *Nothofagus nitida* and *Fitzroya cupressoides* formations. Throughout zone A the predominant soils are deep brownish acid soils with variable podsolization; the most extreme acidity and podsolization, in some cases reaching peat, is observed under the *Fitzroyetum cupressoidis* formations in hill-top flat sites.

In zone B, the Andean Piedemontes, *Nothofagus nitida* woodlands are found on volcanic substrates ranging from trumaos to ñadi soils (Donoso, 1989), although in view of the hygrophilous nature of *Nothofagus nitida* it frequently occurs in soils with some degree of waterlogging and strong acidification of organic matter, typically in association with

Tepualia stipularis. Holdgate (1961) studied soils under *Nothofagus nitida* woodland with *Tepualia stipularis* on Chiloé island, observing variable peat depth and marked acidity (mean pH 4.0).

There is little data available on the soils under woodlands in Zone C. Holdgate (1961) prospected in Puerto Edén, at the extreme southern range of *Nothofagus nitida* (49° 08' S), and again found peaty soils with marked acidity, although the *Nothofagus* woodlands defined by this author as a vegetation type contained a mixture of *Nothofagus nitida* and *Nothofagus betuloides*, which in phytosociological terms is perhaps better interpreted as *Nothofagetum betuloidis*. It thus seems likely that in this entire territory between the south of Chiloé Island (43° S) and the southern limit of *Nothofagus nitida* (49° S), this species occurs largely on peaty soils, with peat depth depending on topography. Weinberger (1973) referred to *Nothofagus nitida* on southern Chiloé Island as "the tree of the flats and permanently wet soils along the coast".

III. METHODOLOGY

A total of 40 relevés were obtained from woodland sites as undisturbed as possible, from physiographic zones A and B (Coastal Range and Piedemontes), in all cases selecting sites at which *Nothofagus nitida* was the dominant species. Relevés were obtained in accordance with classical Braun-Blanquet methodology (Braun-Blanquet, 1979) as modified by Géhu & Rivas-Martínez (1981).

To avoid sampling at sites transitional to other vegetation types (particularly woodlands with other coihue species), we selected areas or altitudinal belts in which *Nothofagus nitida* is clearly the dominant tree. We preferentially selected sites with mature trees, with *Nothofagus nitida* making up at least 20-25% of cover. Some sites were second-growth woodland, but with high *Nothofagus nitida* cover. Plot area ranged from 100 to 500 m^2.

For characterization of structure, we considered plots to comprise a tree stratum (E_1) and a shrub stratum (E_2). We calculated both tree cover (E_1 cover) and tree/shrub cover (E_1 cover + E_2 cover). The tree/shrub stratum was defined as that above 3 m height, 3 m being the normal maximum height of quilas (*i.e. Chusquea* sp. pl.). Cover data for these strata are shown in Table I, though note that the indices of abundance shown for individual tree species correspond either to E_1 cover or E_2 cover, whichever was highest; indices of abundance did not consider either seedlings or saplings.

In three areas we performed a more detailed analysis of structure, marking out a plot of 20 x 20 m^2 in which we measured the diameter at breast height (DBH) of all trees with DBH > 10 cm. These three plots were selected as representative of the structural variability of the whole sample; they were at the same sites as (though not precisely coincident with) three of the relevé plots. Schematic diagrams were drawn on the basis of DBH and basal area data for each species, since this latter variable is that which shows a most nearly linear relationship with tree age (Innes, 1992).

In the relevé tables, filmy ferns (Hymenophyllaceae) are listed in a separate section, in view of the marked diversity of these species in the hyperhumid woodlands of Chile. The maximum abundance rating for filmy ferns is 2, indicating that the species was very frequent in the relevé, whether on trunks and on the ground.

Using the relevé table data (Table I), a hierarchical classification was obtained by cluster analysis (nearest-neighbour linkage) with squared Euclidean distance as measure of similarity, using the statistics package SPSS (2001). Braun-Blanquet indices of abundance were transformed to numerical values by the method of Van der Maarel (1979).

Taxonomy and nomenclature

All plants in each relevé were identified to species level, following the nomenclature of Marticorena & Quezada (1985) and Marticorena & Rodríguez (1995, 2001). Taxonomically problematic taxa are as follows.

First, and in line with the criteria proposed by Matthei (1997), the quilas (*Chusquea* sp. pl.) present in our relevés are of two taxa: *C. valdiviana* and *C. uliginosa*. Above 600 m altitude, most quilas are probably *C. uliginosa*, with *C. valdiviana* at lower altitudes. However, these two species are often difficult to distinguish in the field, and they are thus listed together in the table.

Second, some infertile individuals of *Gleichenia* in relevés in the Coastal Range were difficult to assign (to *G. squamulosa* or *G. litoralis*), suggesting that the two species may coexist. In our view, and at least in the Piedemonte zone of mainland Chiloé and Aysén, the most frequent species is *G. litoralis*: given the identification difficulties, however, we list these two taxa together in Table I. In any case, the important point is that *G. squamulosa* and/or *G. litoralis* are present in the new association, and not in phytosociologically related communities (see Table II).

Third, *Nothofagus betuloides* is indicated as possibly present in relevé 37, because the individuals in question showed anomalous leaf characteristics suggesting a possible *Nothofagus nitida* x *betuloides* hybrid. This possibility is plausible, since numerous individuals of *N. betuloides* are present on the hill-top close to this relevé, and hybridization between these two species has been reported previously in areas in which they are sympatric (Donoso & Atienza, 1984).

For identification of filmy ferns we followed the criteria of Diem & Lichtenstein (1959), although adapted to the systematic scheme proposed by Rodríguez (1995).

Syntaxonomic nomenclature is in all cases in line with the 3rd edition of the Code of Phytosociological Nomenclature (Weber *et al.*, 2000).

IV. RESULTS

After prospecting woodlands dominated by *Nothofagus nitida*, and although we have not prospected the southern part of this species' range, we consider that there are clearly sufficient arguments for defining a new association: first, these woodlands show a characteristic floristic composition that is maintained consistently throughout the region, and second, they show well-defined and consistent biogeographic, ecological, structural and dynamic differences with respect to other similar communities.

A. Floristic composition and phytosociology

Table I shows the floristic composition that defines the proposed new association *Luzuriago polyphyllae-Nothofagetum nitidae* ass. nova (holotype relevé n° 18, Table I). This is a woodland community dominated by broad-leaved evergreens together with conifers that reach similar heights but not similar cover values. Also important are lianas like *Campsidium valdivianum*, various subfruticose (*i.e.* small shrub) species capable of climbing on trunks, including species of the genera *Luzuriaga, Griselinia* and *Asteranthera*, and the striking filmy-fern communities showing species diversities not exceeded by any

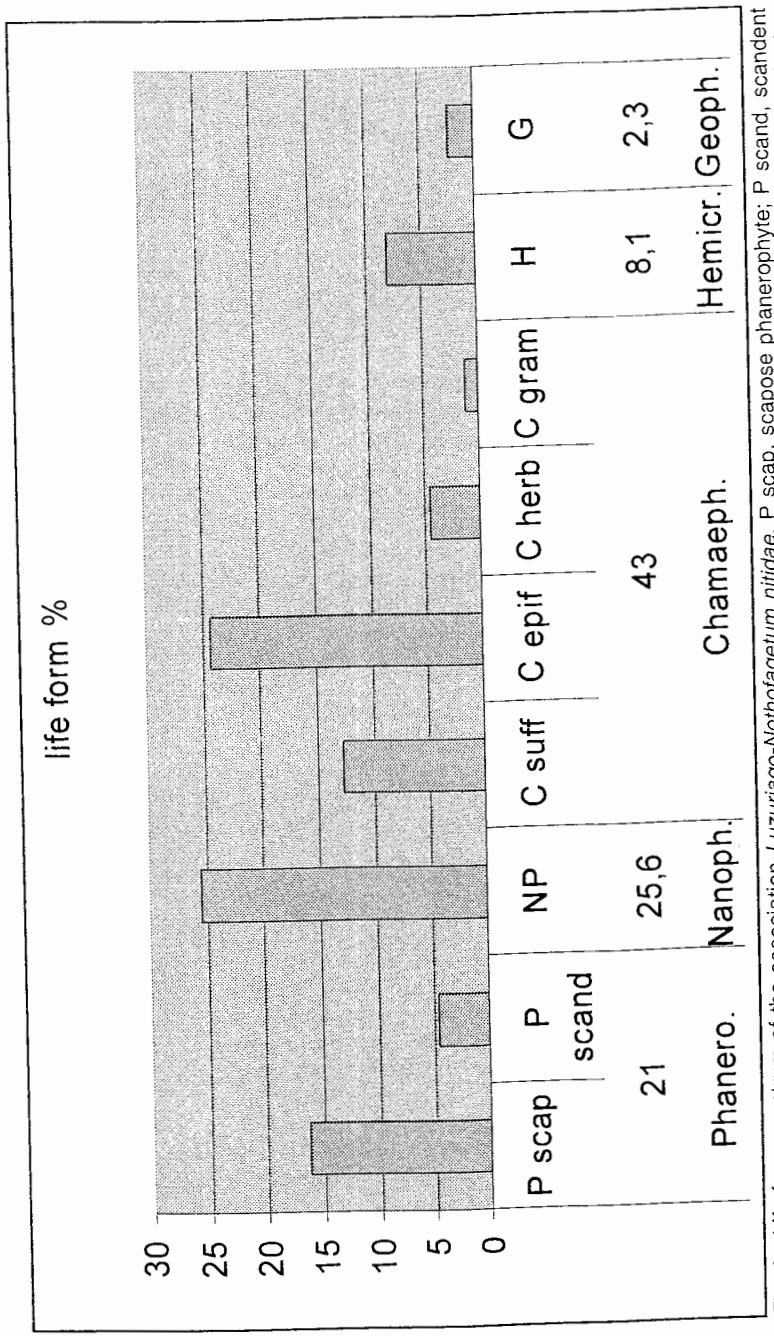


Fig. 3.- Life-form spectrum of the association *Luzuriago-Nothofagetum nitidae*. P scap, scapose phanerophyte; P scand, scandent phanerophyte (lianas); NP, nano-phanerophyte; C suff, subfruticous chamaephyte; C epif, epiphytic chamaephyte; C herb, herbaceous chamaephyte; C gram, graminoid chamaephyte (bamboo); H, hemicryptophyte; G, geophyte.

Fig. 3.- Spectre biologique du *Luzuriago-Nothofagetum nitidae*. P scap, phanérophyte dressé ; P scand, phanérophyte grimpant (liane) ; NP, nano-phanérophyte ; C suff, chaméphyte suffrutescent ; C epif, chaméphyte épiphyte ; C herb, chaméphyte herbacé ; C gram, chaméphyte graminoïde (bambou) ; H, hémicryptophyte; G, géophyte.

other Chilean temperate rainforest. Figure 3 summarizes the life-form composition of the floristic grouping detailed in Table I. The life form assignments are based on Hildebrand-Vogel (2002), who catalogues more than 150 species of the flora of the temperate woodlands of southern Chile; however, we have included an additional category, "epiphytic chamaephyte", for strictly epiphytic ferns such as the hymenophyllaceans, which are abundant in these communities.

The main grouping in Table I (relevés 1-32) represents what we consider to be *Luzuriago polyphyllae-Nothofagetum nitidae* subass. *nothofagetosum nitidae* subass. nova (holotype relevé n° 18, Table I), which occurs practically throughout our study area. However, some of these relevés (n° 1-11, Table I) are representative of a specific situation arising on contact between *Luzuriago-Nothofagetum nitidae* and formations dominated by tepú (the myrtacean *Tepualia stipularis*), which occur in locations with prolonged water-logging, generally in flat valley bottoms. When topography is favourable the area of contact is sufficiently extensive for development of edaphohygrophilous woodland in which *Nothofagus nitida* dominates the upper stratum but in which cover tends to be lower (30-60%). This community, although it is frequent and occupies considerable areas, is clearly transitional between *Luzuriago-Nothofagetum nitidae* and woodlands with edaphically determined distributions (such as *Pilgerodendronetum uviferi*) although we cannot rule out the possible existence of a new community identifiable as "*Tepualietum stipularidis*". In such transitional situations, the most suitable syntaxonomic rank is probably that of variant, *i.e. Luzuriago-Nothofagetum Tepualia stipularis*-variant.

On the other hand we should note an interesting modification of the association biogeographically linked to the Coastal Range, and which has been recorded from close to Valdivia in the north to the Piuchué Range on Chiloé island in the south. These tend to be formations totally dominated by *Nothofagus nitida*, with an understorey containing certain species absent from low-altitude relevés or relevés obtained at some distance from the coast: these include the myrtacean *Ugni candollei*, as well as *Greigia landbecki* and less frequently *Myrceugenia chrysocarpa*. We propose classifying this community as a subassociation *Luzuriago-Nothofagetum nitidae* subass. *ugnetosum candollei* subass. nova (holotype relevé n° 35, Table I).

A key problem in the identification of this new association is that its bioclimatic, catenal and floristic position overlaps with that of three other associations of the *Nothofago-Winterion* alliance: *Laurelio-Weinmannietum trichospermae, Fitzroyetum cupressoidis* and *Pilgerodendronetum uviferi*. This overlap may explain the fact that a separate *Nothofagus nitida* community was not defined either in the first phytosociological synthesis (Oberdorfer, 1960) or in the Forest Types classification (Donoso, 1981). In an attempt to clarify the floristic differences between these overlapping formations, Table II summarizes known published relevés for the associations of this type originally described in the *Nothofago-Winterion* alliance. The table thus includes two associations dominated by other coihues, namely *Chrysosplenio-Nothofagetum dombeyi* and *Nothofagetum betuloidis*, though note that it has recently been proposed that the former be included in a different order (Pollmann, 2001).

B. Structure of the *Nothofagus nitida* woodlands

Strata and species

The general appearance of the *Luzuriago polyphyllae-Nothofagetum nitidae* woodlands is of a rather closed canopy, more homogeneous with increasing dominance of *Nothofagus nitida* in the tree layer. In general, *Nothofagus nitida* shares dominance with individuals of

other less numerous emergent species, such as *Laureliopsis philippiana* (18 relevés) and *Saxegothaea conspicua* (12 relevés), this latter species being that for which highest canopy-layer covers were recorded after *Nothofagus nitida*. The shade-tolerant nature of these two species (Donoso, 1989) that commonly accompany Chiloé coihue supports the idea that, in the early stages of woodland development, cover in the upper canopy layer is almost total, and that subsequently the felling of coihues or fall of large individuals in storms favours the installation of these species in the resulting clearings, where they may reach heights similar to those reached by *Nothofagus nitida* (Veblen *et al.*, 1996; Lusk, 1999). In the case of *Drimys winteri*, entry into the upper layer has been in recovery woodlands following clearance felling a long time previously, so that it only reaches heights similar to *Nothofagus nitida* in immature situations. Rather more characteristic in appearance is the canopy of the *Tepualia stipularis*-variant when cover by this arborescent species (reaching up to 15-18 m) is relatively high: in such cases the erect-patent cauline ramification of this myrtacean, together with the rather low density of its leaf organization, mean that the canopy has a highly characteristic open and irregular appearance.

The upper stratum (E_1) is almost never continuous, but when the lower stratum E_2 is taken into account, total cover may reach 90-100%, heavily shading the understorey. Only in three relevés (4, 5 and 9; Table I) of the 40 considered were E_1+E_2 cover values lower than 90%, and all three relevés are of the *Tepualia stipularis*-variant. An idea of the vertical structure of the woodland is given in Figure 4; although the relevés were of different ages (with significant among-relevé differences in canopy height ranges), tree sizes within a given relevé generally show more or less continuous variation, except in some woodlands dominated by mature trees of closely similar age (*e.g.* relevés 30, 38, 40), and in some of the *Tepualia stipularis* woodlands (relevés 4 and 9). The largest shrub species in E_2 are *Amomyrtus luma* and *Caldcluvia paniculata*, followed by *Lomatia ferruginea* or *Crinodendron hookerianum*; however, the highest covers in this layer are from species

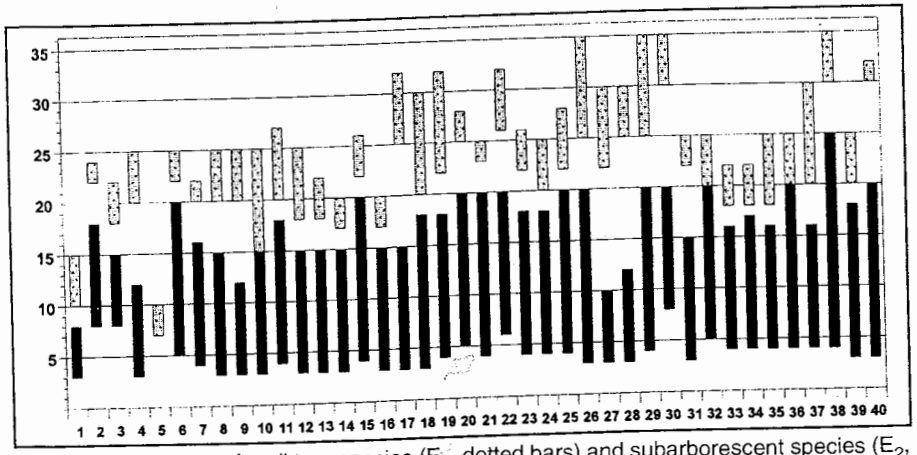


Fig. 4.- Height ranges for all tree species (E_1, dotted bars) and subarborescent species (E_2, dark bars) in each of the 40 relevés from Table I.

Fig. 4.- Rangs des hauteurs mesurées pour les différents espèces d'arbres (E_1, barres ponctuées) et arbres inférieurs (E_2, barres foncées) dans les 40 relevés du Tableau I.

capable of reaching the upper canopy (*Drimys winteri, Podocarpus nubigena* and *Laureliopsis philippiana*, in decreasing order of frequency). This layer sometimes contains (though with low frequency) potentially emergent species that may indicate possible transitions to other communities: *Nothofagus betuloides* (relevés 27, 28, 32 and 37), *Fitzroya cupressoides* (relevés 6 and 37) and *Eucryphia cordifolia* (relevés 8, 9, 13, 14, 16, 20 and 24).

Trunk diameters and basal areas

The three plots selected for trunk diameter and basal area measurements correspond to relevés 24, 31 and 38, bearing the typical subassociation (plots 1 and 2) or the subassociaton *ugnetosum candollei* (plot 3). We did not obtain similar data from a *Tepualia stipularis* variant plot, because the pluricauline architecture of tree-size individuals of *T. stipularis* means that "trunk diameter" cannot meaningfully be measured.

The data for the three plots (summarized in Table III and Fig. 5) allow the following conclusions to be drawn. First, there are always several tree or arborescent species, between 4 and 6 individuals in these plots, up to 9 in some plots. Second, *Nothofagus nitida* is dominant in terms of basal area (54-73% of total basal area); the other large species most frequently present is *Laureliopsis philippiana* (generally fewer individuals than *N. nitida*). Third, some plots have mature trees with high diameter at breast height (DBH) and no regeneration (plot 3, Fig. 5C), but in most cases a range of DBHs are present, indicating regeneration (see Figs. 5A and 5B). Fourth, total basal area (indicative of timber density) was high in all three plots (114-178 $m^2.ha^{-1}$). Innes (1992) reported his own and previously published data indicating total basal areas of 90-100 $m^2.ha^{-1}$ for well-conserved Chilean temperate rainforest plots between 41 and 46° S; in contrast, degraded woodlands from the same territory show values of 30-45 $m^2.ha^{-1}$. By comparison, Veblen *et al.* (1996) repor-

Table III.- Dendrometric data (diameter at breast height, DBH, cm, and basal areas, BA, m^2) in three selected plots. NI = no. of individuals of each species with DBH > 10 cm. minimum (DBH_{min}) and maximum (DBH_{max}) DBH values in each plot are also shown. BA was calculated as $\pi(DBH/2)^2$.

Tableau III.- Données dendrométriques (diamètre à hauteur de poitrine, DBH en cm, et surface de base, BA, m^2) tirées de trois parcelles choisies. NI = nombre d'individus de chaque espèce à DBH > 10 cm. Les valeurs du DBH minimum (DBH_{min}) et maximum (DBH_{max}), pour chaque espèce et à chaque parcelle, sont aussi exprimées. Le calcul du paramètre BA est $\pi(DBH/2)^2$.

	Plot 1 (relevé 24, Tb. I)					Plot2 (relevé 31, Tb. I)					Plot 3 (relevé 38, Tb. I)				
Species	N. I.	DBH. min	DBH max.	Basal area	%	N. I.	DBH min.	DBH max.	Basal Area	%	N. I.	DBH min.	DBH max.	Basal Area	%
Nothofagus nitida	12	12.1	129.2	3.36	66.0	16	23.2	60.2	2.50	54.7	15	43.6	81.2	5.22	73.3
Drimys winteri	27	10.2	36.6	1.04	20.4	20	12.1	50.3	1.62	35.4	.	.	.	.	.
Laureliopsis philippiana	1	56.9	56.9	0.26	5.1	4	15.9	45.2	0.37	8.1	19	13.4	42.6	1.17	16.4
Caldcluvia paniculata	11	10.2	34.7	0.39	7.7	.	.	.	.	.	.	.	.	.	.
Amomyrtus luma	1	11.1	11.1	0.01	0.2	3	13.4	24.2	0.08	1.8	.	.	.	.	.
Luma apiculata	1	19.4	19.4	0.03	0.6	.	.	.	.	.	.	.	.	.	.
Saxegothaea conspicua	.	.	.	.	.	.	.	.	.	.	20	10.2	36.3	0.63	8.9
Podocarpus nubigena	.	.	.	.	.	.	.	.	.	.	2	14.6	33.1	0.10	1.4
Total plot (400 m^2)				5.09					4.57					7.12	
m^2/ha				127.2					114.2					178	

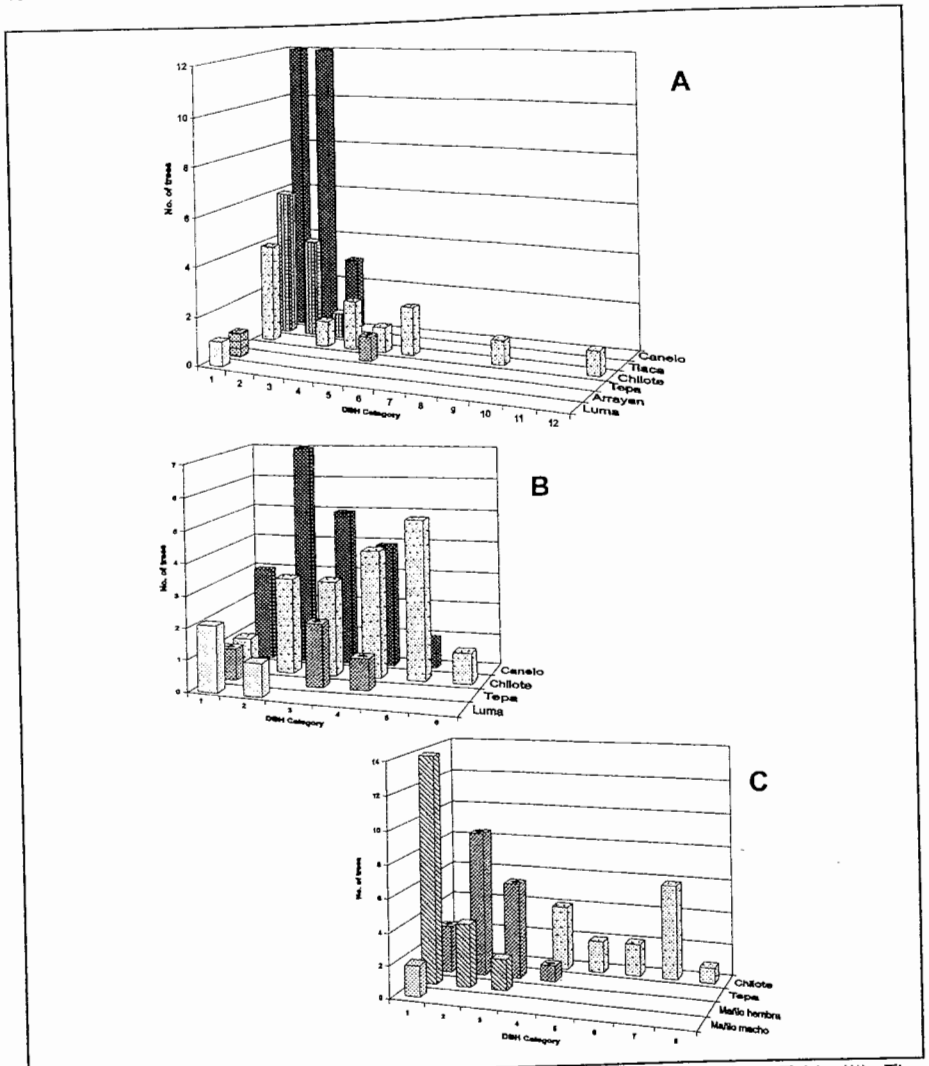


Fig. 5.- Size distributions of major tree species in plots A, B and C (see Table III). The figures show number of individuals in each DBH category (DBH = diameter at breast height; category 1 DBH 10-20 cm, category 2 DBH 20-30 cm, etc.). Species are indicated by their local names: Canelo = *Drimys winteri*; Tiaca = *Caldcluvia paniculata*; Chilote = Coihue de Chiloé = *Nothofagus nitida*; Tepa = *Laureliopsis philippiana*; Arrayán = *Luma apiculata*; Luma = *Amomyrtus luma*; Mañío hembra = *Saxegothaea conspicua*; Mañio macho = *Podocarpus nubigena*.

Fig. 5.- Diagrammes structuraux des trois carrés étudiés en détail (cf. Tableau III). Les figures rapportent le nombre d'individus appartenant à chaque rang de DBH (DBH = diamètre à hauteur de poitrine ; rang 1 : DBH 10-20 cm, rang 2 : DBH 20-30 cm, etc.). Les espèces sont nommées selon leur mot local : Canelo = *Drimys winteri* ; Tiaca = *Caldcluvia paniculata* ; Chilote = Coihue de Chiloé = *Nothofagus nitida* ; Tepa = *Laureliopsis philippiana* ; Arrayán = *Luma apiculata* ; Luma = *Amomyrtus luma* ; Mañío hembra = *Saxegothaea conspicua* ; Mañío macho = *Podocarpus nubigena*.

ted a maximum value of 160 $m^2.ha^{-1}$ for mixed *Nothofagus* woodland in southern Chile, while Ogden *et al.* (1996) reported 150 $m^2.ha^{-1}$ for *Nothofagus* woodlands with or without conifers in New Zealand.

Understorey

Although we have not performed a quantitative survey of seedling and sapling presences, we observed and annotated the regeneration of tree species in the understorey. Clearly important species are *Drimys winteri, Laureliopsis philippiana, Amomyrtus luma* and *Caldcluvia paniculata*, which show regeneration in all relevés in which they were also present in the upper strata; somewhat lower but still marked regeneration were shown by *Lomatia ferruginea* (92%), *Saxegothaea conspicua* (90%) and *Podocarpus nubigena* (60%). *Nothofagus nitida* was detected in the understorey layer in only 35% of relevés, but this figure may be misleading in that this species commonly regenerates in clearings with no shrub or tree cover, whereas we deliberately selected plots with dense canopies for our relevés. Interestingly, the presence of *Nothofagus nitida* seedlings within the dense woodland was always accompanied by old fallen trunks, as reported in previous studies (Lusk, 1995, 1996; Veblen *et al.*, 1996).

Thus a well-shaded understorey, together with the strongly ombrophilous nature of *Luzuriago polyphyllae-Nothofagetum nitidae*, means that the interiors of these woodlands usually have rather dense shrub and epiphyte floras, as well as high moss and filmy fern covers. The synusiae formed by these ferns are particularly important in woodlands of this type, in which they may occur both on the ground and on trunks, forming dense mats extending up to 20 m above ground level.

Cluster analysis of the relevés

To support the objective validity of the phytosociological classification, we performed a hierarchical clustering of the 40 relevés on the basis of their floristic characteristics. The results of this analysis are shown graphically in Fig. 6. Major points to be noted as follows.

Firstly, the relevés of the subassociation *nothofagetosum nitidae* are mostly grouped together (branch A-2), and within this branch nearly all of the relevés of the hygrophilous *Tepualia stipularis*-variant (relevés 1-9) are grouped into a discrete category (branch A-2b).

Secondly, four relevés of the subassociation *nothofagetosum nitidae* are grouped apart from the rest and together with those of subassociation *ugnetosum candollei* (*i.e.* in branch A-1). All of these four relevés are at altitudes of between 600 and 715 m, and except n° 26 are all in the Coastal Range, so that biogeographically and floristically they are very close to the subass. *ugnetosum candollei*. In fact relevés 29 and 32 include *Greigia landbeckii*, one of the differential species of this community.

Thirdly, five relevés were classified by the cluster analysis as different from the rest (branches B and C). The inclusion of relevés 17, 27 and 28 in these branches is attributable to the fact that they are all from the Queulat National Park where the combination of latitude and altitude situates these relevés in a position rather distant from the floristic optimum of *Luzuriago-Nothofagetum*, and in fact rather closer to that of *Nothofagetum betuloidis*, which replaces *Luzuriago-Nothofagetum* in this National Park between about 500 m and the tree limit.

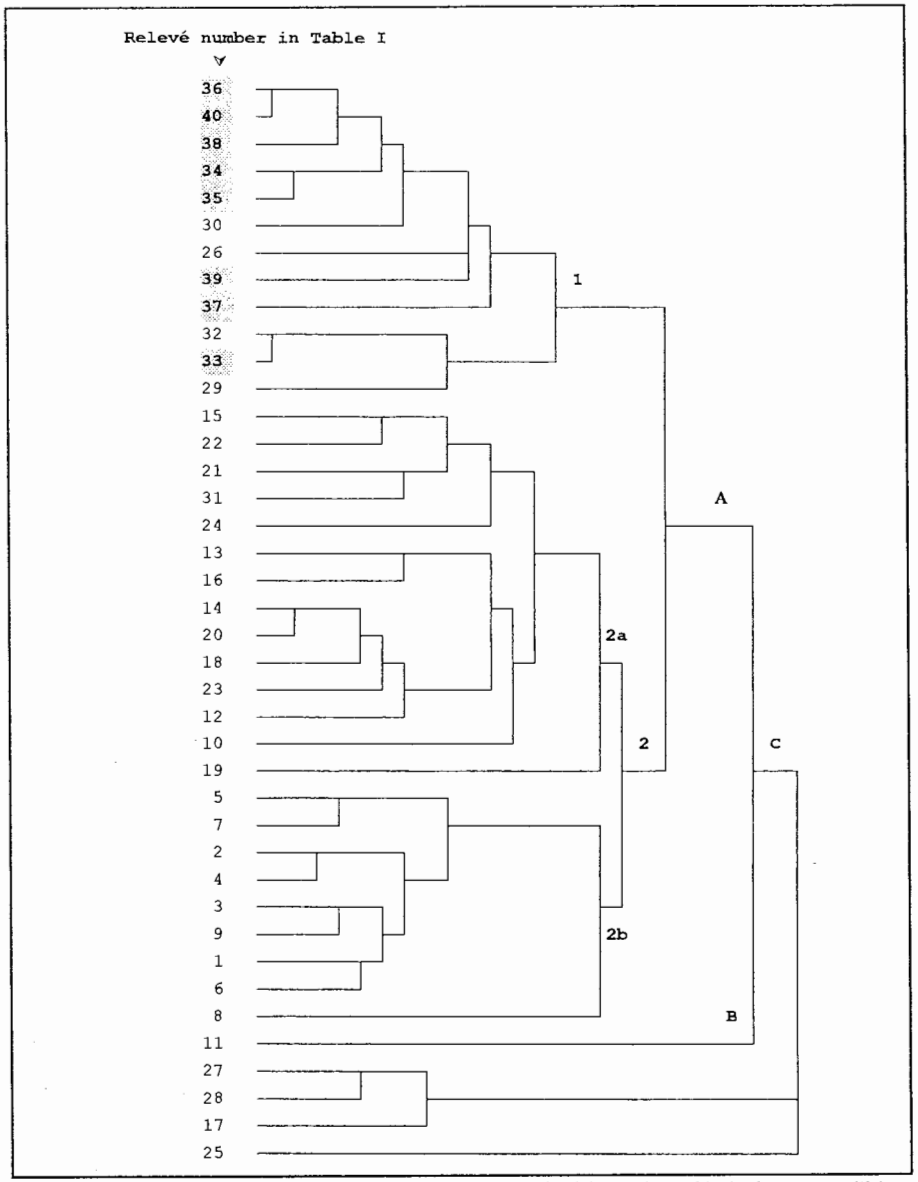


Fig. 6.- Results of hierarchical clustering (dendrogram) of *Luzuriago-Nothofagetum nitidae*. Numeration agrees with Table I (for details, see Methodology). Shaded numbers mark: relevés of subass. *ugnetosum candollei*.

Fig. 6.- Dendrogramme hiérarchique des relevés du *Luzuriago-Nothofagetum nitidae*. La numération des relevés est celle du Tableau I (voir Méthodologie). Numéros grisés : relevés de la sous-association *ugnetosum candollei*.

V. DISCUSSION

A. Phytogeographic aspects

Since *Nothofagus nitida* is a Chilean endemic, the new association described here is likewise endemic. This association has been detected to at least 44° 40' S, at the level of Puerto Cisnes, but previous reports suggest that it may occur even further south (for example the woodlands studied by Innes 1992 in the Tai-Tao peninsula very close to 46° 30' S).

However, although *Nothofagus nitida* extends as far south as the 49th parallel, it is still not possible to precisely evaluate how much area might be occupied by these *Luzuriago-Nothofagetum* woodlands, and how much area by woodlands in which both coihue species of this region are present (*Nothofagus betuloides* and *Nothofagus nitida*). Communities of the latter type should be interpreted as *Nothofagetum betuloidis*, in view of the floristic composition of this association as originally described. For Donoso (1993), all of the oceanic territory corresponding to that here denominated the Aysén channels zone from the 47th parallel southwards bears the Magallanes Coihue forest type (*i.e.* woodland dominated by *N. betuloides*).

It is however important to stress that the overall distribution of *Nothofagus nitida* is rather different from that given in CONAF (1998): specifically, its distribution in the Andean foothills is more restricted than suggested by the CONAF report. This conclusion is based on our field prospecting in the territory between Puerto Montt and Puerto Aysén, and is in line with previous reports: see for example McQueen's (1977) comments on the distribution of *Nothofagus nitida* to the south of Puerto Montt, and Gajardo's (1994) vegetation map of the 11th region.

B. Ecological aspects

All forms of *Luzuriago-Nothofagetum nitidae* are woodlands requiring very high rainfall, though in relatively low-rainfall areas "edaphic compensation" may be observed (*i.e.* localization in sites with more or less permanent waterlogging of the soil). The capacity of *Nothofagus nitida* to tolerate temporary waterlogging (as commonly observed in communities with *Tepualia stipularis*) has been noted previously by Holdgate (1961), who studied woodlands on fluvial terraces of the lowest altitudinal belt, at the mouth of the river Chepu in the north of Chiloé island. Godley (1960) noted that this characteristic of *Nothofagus nitida* constitutes an ecological separation from the Valdivian woodland ("*Eucryphia-Laurelia-Weinmannia* forest") present in this territory, since this latter occupies well-drained slopes while *Nothofagus nitida* grows on more acid and less well-drained soils. Both *Tepualia stipularis* and *Myrceugenia parvifolia* are good indicators of the degree to which gleyzation occurs in the azonal woodlands we denominate *Luzuriago-Nothofagetum, Tepualia stipularis*-variant. Weinberger (1978) notes these two myrtaceans as the most hygrophilous of those occurring in Chile, and likewise the most dependent on high atmospheric humidity.

The optimal position for *Luzuriago-Nothofagetum nitidae*, in terms of the bioclimatic classification of Rivas-Martínez (1995), is in the upper sub-belt of the Mesotemperate belt, extending into the Supratemperate belt. As regards rainfall, the optimal position is the Ultrahyperhumid belt (Amigo & Ramírez, 1998). However, it is not only the high precipitation that defines the requirements of these *Nothofagus nitida* woodlands, but also the permanently high atmospheric humidity, probably reflecting the weak horizontal root system of this species (Weinberger, 1973). This intolerance of atmospheric dryness places

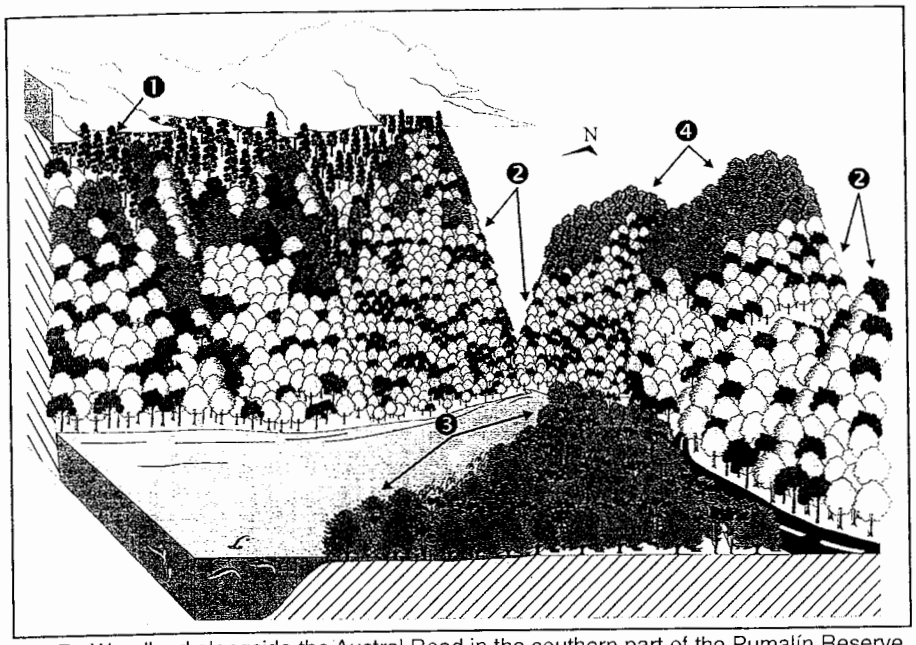


Fig. 7.- Woodland alongside the Austral Road in the southern part of the Pumalín Reserve, on the banks of the Rio Negro Lake, in Palena Province, Region de Los Lagos (see Discussion at point B). The different woodland communities are indicated as follows: ① *Fitzroyetum cupressoidis*, ② *Laurelio-Weinmannietum trichospermae*, ③ *Luzuriago-Nothofagetum nitidae* var. *Tepualia stipularis*, ④ *Luzuriago-Nothofagetum nitidae* typical ass.

Fig. 7.- Distribution paysagère des groupements forestiers au sud du parc Pumalín, aux alentours du lac Río Negro, province de Palena, région de Los Lagos (voir Discussion, B). ① *Fitzroyetum cupressoidis*, ② *Laurelio-Weinmannietum trichospermae*, ③ *Luzuriago-Nothofagetum* var. à *Tepualia stipularis*, ④ *Luzuriago-Nothofagetum* typique.

Nothofagus nitida at a disadvantage with respect to *N. dombeyi*, so that in the zone we denominate Piedemontes *Nothofagus nitida* occurs close to the coast, while further inland (or in areas in which there are significant topographic barriers to the influx of oceanic air masses) it is replaced by *N. dombeyi*, in pure stands or in association with *Laurelio-Weinmannietum* (see Fig. 7).

Extremely peaty soils are not favourable for *Luzuriago-Nothofagetum nitidae*: in such situations it is generally replaced by communities dominated by the hygrophilous cupressaceans *Fitzroya cupressoides* and *Pilgerodendron uviferum*. Clearly, transition environments often occur between poorly drained soils with more or less prolonged waterlogging (which, as noted, are acceptable for *Luzuriago-Nothofagetum nitidae*) and peaty soils showing classic histosol characteristics and the presence of differential species of the class *Myrteolo-Sphagnetea*: in such transitional environments, attempts at phytosociological classification on the basis of the dominant tree are likely to be unreliable. An example of a community intermediate between *Luzuriago-Nothofagetum nitidae* and *Fitzroyetum cupressoidis* was reported by Donoso *et al.* (1990) under the denomination "Alerce-Chiloé Coihue forest subtype" (see comments below in Section D Syntaxonomic aspects).

In areas with marked oceanic influx, such as the south of Chiloé island, formations classifiable as *Pilgerodendronetum uviferi* are frequent, and the constant presence of *Tepualia stipularis* in these formations has meant that they are referred to by the vernacular name tepual; Veblen *et al.* (1983), in their forest type n° 5, reported tepuales present in sites in southern Chile adjacent to *Nothafagus nitida* woodlands in positions with better drainage. This description appears to presage the community which we denominate *Luzuriago-Nothofagetum, Tepualia stipularis*-variant.

The association with which *Luzuriago-Nothofagetum* shows greatest floristic similarity and with which it contacts most frequently is *Laurelio-Weinmannietum trichospermae*; in fact this community is that which replaces *Luzuriago-Nothofagetum* at lower altitudes in the typical catenas of the Pelada Range (Ramírez *et al.*, 1996). Transitional ecotones between these associations are frequent throughout the territory considered in the present study. The transition from *Luzuriago-Nothofagetum* to *Laurelio-Weinmannietum* is usually attributable to lower rainfall, in line with the higher tolerance of *Laurelio-Weinmannietum* to fluctuations in atmospheric humidity, as noted by Weinberger (1973) in his discussion of the differing microclimatic requirements of *Nothofagus nitida* and *N. dombeyi*.

A good example of the way in which these two associations separate is shown in Fig. 7, corresponding to the surroundings of lake Río Negro (42° 42' S; see Fig. 1): this is a flat-bottomed valley with north-south orientation, bounded by steep slopes, with a mountain chain reaching higher altitudes (up to 1200 m a.s.l.) in the west than in the east. In this topographic situation, the rainshadow effect leads to a *Fitzroyetum/Luzuriago-Nothofagetum/Laurelio-Weinmannietum* sequence down the slope on the west side; the *Fitzroyetum* woodland is abundant on the very rainy hilltops, and descends some distance downslope along streambanks with high soil moisture content. At lower levels the topography and rainshadow allow patches of *Luzuriago-Nothofagetum* to grow on slopes otherwise largely covered by *Laurelio-Weinmannietum*. In addition, it can be seen that in the higher parts of the eastern end of the valley, the hill tops are not sufficiently wet and cool for *Fitzroyetum*, and are thus colonized by *Luzuriago-Nothofagetum*, while the hill-slopes and valley bottom (receiving lowest rainfall) are occupied by *Laurelio-Weinmannietum*. Finally, the valley bottom (with negligible slope and accumulation of fine sediments) forms a sporadically flooded floodplain around the shores of the lake, creating perfect edaphic conditions for the *Tepualia stipularis*-variant of *Luzuriago-Nothofagetum*.

C. Filmy ferns

Detailed data indicating which Chilean rainforest communities are richest in hymenophyllaceans are not yet available. However, the bioclimatic position and territorial range of *Luzuriago-Nothofagetum nitidae* suggest that it is an ideal habitat for these species. A total of 3 genera and 24 species of this family are present in Chile (Rodríguez, 1995). Three of these species are endemic to the Juan Fernández archipelago, so that mainland Chile has a total of 21 species, at least 17 of which occur in *Nothofagus nitida* woodlands. As shown in Table II, filmy fern species diversity in the different *Nothofago-Winterion* communities is highest in the various forms of *Luzuriago-Nothofagetum nitidae*, and is otherwise approached only in *Laurelio-Weinmannietum* subass. *luzuriagetosum polyphyllae* (described as the most oceanic form of this association). The fact that these are the only communities within the alliance that may contain species like *Hymenoglossum cruentum* or *Hymenophyllum caudiculatum* constitutes an additional argument in favour of the oceanic

character of these communities, since these two species are particularly sensitive to atmospheric dryness, as demonstrated in laboratory trials with a range of hymenophyllaceans from thermophilous Valdivian woodland (Alberdi *et al.*, 1978).

The abundance and diversity of these pteridophytes in our relevés are also an indication of the good conservation of most of the plots studied. Ramírez *et al.* (1976) showed that the number of epiphytic hymenophyllaceans on trunks in a Valdivian woodland declined dramatically after partial felling.

The synusiae constituted by these ferns in woodland sites, together with abundant bryophytes, form dense mats on the trunks of mature trees, as well as on stumps and fallen logs. With the slow decomposition of stumps and logs, these fern/bryophyte mats persist on the litter layer. Several authors have argued that these synusial communities provide important information on the ecological and biogeographic nature of these woodlands (*e.g.* Riveros & Ramírez, 1978; Schuhwerk, 1986).

D. Syntaxonomic aspects

The floristic composition of the relevé group shown in Table I leaves no doubt that it should be assigned to the alliance *Nothofago-Winterion*, given the presence of *Desfontainia spinosa, Asteranthera ovata, Philesia magellanica, Blechnum magellanicum, Podocarpus nubigena, Campsidium valdivianum, Grammitis magellanica* and *Maytenus magellanica*.

Table IV.- Summarized differences between *Luzuriago polyphyllae-Nothofagetum nitidae* and the various associations of *Wintero-Nothofagetalia* with which it may show catenal contact.

Tableau IV.- Diférenciation du *Luzuriago polyphyllae-Nothofagetum nitidae* relativement aux autres associations des *Wintero-Nothofagetalia* en contact catenal.

In comparison with *Luzuriago-Nothofagetum nitidae* ▼	*Laurelio-Weinmannietum trichospermae*	*Fitzroyetum cupressoidis*	*Pilgerodendronetum uviferi*	*Nothofagetum betuloidis*
Is generally....	less ombrophilous (*i.e.* tolerates lower rainfall)	more orophilous (*i.e.* locates at higher altitudes)	totally azonal (always occurs in edaphohygrophilous positions)	more cryophilous(*i.e.* tolerates colder temperature regimes)
Is also...	more tolerant of continental climate (*i.e.* tolerates wider thermal amplitude)	more tolerant of continental climate (*i.e.* tolerates wider thermal amplitude)	A swampy woodland of permanently waterlogged soils	Its ecological vicariant (replacing *Luzuriago-Nothofagetum* south of the 47th parallel)
May also be...	more thermophilous (*i.e.* locates at lower altitudes)	more peat-tolerant (*i.e.* tolerates waterlogged soils like those of *Pilgerodendronetum*)	more boreal (present until Tierra de Fuego to 54° S)	more boreal (present in Tierra de Fuego to 55° S)
Unlike *Luzuriago-Nothofagetum nitidae* ▼	*Laurelio-Weinmannietum trichospermae*	*Fitzroyetum cupressoidis*	*Pilgerodendronetum uviferi*	*Nothofagetum betuloidis*
May contact with...	communities of *Nothofagetea pumilionis*	communities of *Nothofagetea pumilionis*	communities of *Myrteolo-Sphagnetea*	communities of *Nothofagetea pumilionis*, communities of *Myrteolo-Sphagnetea*
Contains (or often contains) the species...	*Nothofagus dombeyi* (*Dasyphyllum diacanthoides*)	*Fitzroya cupressoides* *Nothofagus dombeyi* (*Drimys andina, Nothofagus pumilio*)	*Pilgerodendron uviferum* *Nothofagus antarctica* (*Nothofagus dombeyi*)	*Nothofagus betuloides* *Berberis ilicifolia* *Escallonia serrata*
Lacks....	*Crinodendron hookerianum* *Gleichenia litioralis* + *Gleichenia squamulosa*	*Crinodendron hookerianum* *Caldcluvia paniculata* *Griselinia ruscifolia*	*Myrceugenia planipes* *Hymenoglossum cruentum* *Hymenophyllum caudiculatum*	*Saxegothaea conspicua* *Campsidium voldivianum* *Laureliopsis philippia-*

Our separation of *Luzuriago-Nothofagetum nitidae* from previously described associations of this alliance is justified in Table II and, more schematically, in Table IV. Certain species presences are discriminant for *Luzuriago-Nothofagetum*, such as *Crinodendron hookerianum, Myrceugenia parvifolia* or the pair *Gleichenia squamulosa* / *G. litoralis*, though the ecological requirements of this latter pair may also be met in *Pilgerodendronetum uviferi* or *Nothofagetum betuloidis*; it seems likely that their apparent absence from these associations (as shown in Table II) reflects previous misidentifications as *Gleichenia quadripartita*. Despite the fact that *Nothofagetum betuloidis* and *Pilgerodendronetum uviferi* are the two associations in which *Nothofagus nitida* occurs most frequently, the floristic separation of each from *Luzuriago-Nothofagetum nitidae* should not cause additional problems: in addition to the tree species *Nothofagus betuloides*, the species *Berberis ilicifolia, Escallonia serrata* and *Luzuriaga marginata* all identify *Nothofagetum betuloidis*, while *Pilgerodendron uviferum* and *Nothofagus antarctica* identify *Pilgerodendronetum*, together with *Lebetanthus myrsinites* which is a good differential of both *Nothofagetum betuloidis* and *Pilgerodendronetum* with respect to other associations (Table II, columns 1, 2 and 3).

The separation of *Luzuriago-Nothofagetum nitidae* and *Fitzroyetum cupressoidis* is rather more complicated. Catenal contact between formations dominated by *Nothofagus nitida* and others dominated by *Fitzroya cupressoides* has been noted in various areas of the Coastal Range [Pelada Range: Veblen & Ashton (1982), Ramírez *et al.* (1996), Devall *et al.* (1998); Piuchué Range: Armesto *et al.* (1996)]. In the original description of *Fitzroyetum cupressoidis*, the only species of *Nothofagus* frequently present is *N. dombeyi* (see Table II, column 11), but alerce woodlands with abundant *N. nitida* in the understorey (Table II, column 7) have also been recorded. In the forestry classification of Donoso *et al.* (1990), with its basically practical intent, a subtype denominated "Alerce-Coihue de Chiloé" is identified within the Alerce forest type, exemplified by a stand in the Andes in which *Fitzroya cupressoides* constituted 18% of the number of trees per ha, versus 21% N. nitida and 61% other trees. However, in terms of phytosociology and ecology (as opposed to practical forestry) this situation is probably better interpreted as transitional between *Fitzroyetum* and this association (of uncertain assignment, since Donoso *et al.* do not specify either the species making up 61% of the total or the species in the understorey).

In other words: the fact that there are situations with little *Fitzroya cupressoides* cover and higher *Nothofagus nitida* cover (for example) means that this can be interpreted as "*Nothofagetum nitidae* in transition to *Fitzroyetum*", not just as *Fitzroyetum*, and not only because *Fitzroya cupressoides* is a taller tree or that which provides most timber per unit surface area. Similarly, the situation studied by Tomaselli (1981) - *i.e. Fitzroya* woodlands in poorly drained soils in association with *Pilgerodendron uviferum*, denominated by this author "*Fitzroyetum pilgerodendronetosum*" (Table II, column 8) - is not incompatible with the existence of *Fitzroyetum cupressoidis* on the one hand and *Pilgerodendronetum uviferi* on the other.

The association with which *Luzuriago-Nothofagetum nitidae* probably shows most similarities is *Laurelio-Weinmannietum trichospermae*; for example, these two associations are practically unique within the *Nothofago-Winterion* in that they may sometimes show species of *Nothofago-Eucryphion*. *Laurelio-Weinmannietum trichospermae* was described by Oberdorfer (1960) with two subassociations, although without typification: the more oceanic *luzuriagetosum erectae*, present in the Coastal Range and Chiloé island, and *philesietosum magellanicae*, present in the Andes and Andean foothills (Table II, columns 13 and 14). This second subassociation shows more frequent presences of species of *Nothofago-*

Winterion than *luzuriagetosum ereciae*, but both contain *Nothofagus dombeyi* with high constancy, and both lack *N. nitida* as well as the other species we have selected as differentials in Table II (*Gleichenia-Crinodendron-Myrceugenia*). To these we may add *Dasyphyllum diacanthoides*, irregularly present in *Laurelio-Weinmannietum* but never present in *Luzuriago-Nothofagetum nitidae*.

A different question is to which order *Luzuriago-Nothofagetum nitidae* (and its alliance *Nothofago-Winterion*) should be assigned. Originally, Oberdorfer (1960) recognized two suballiances within *Nothofago-Winterion*, *Weinmannienion trichospermae* and *Nothofagenion betuloidis*, this latter including only *Nothofagetum betuloidis*; but the alliance was maintained within the order *Laurelietalia philippianae*. In a later study of Magellanic woodlands, Roig *et al.* (1985) offered a more diversified classification of the evergreen woodlands, recognizing two alliances, *Embothrio-Nothofagion betuloidis* and *Nothofagion betuloidis*; at the same time they defined a new order including both alliances, denominated *Wintero-Nothofagetalia betuloidis*. Finally, Pollmann (2001) adopted the new order proposed by Roig *et al.* (1985), but included within it all the associations of *Weinmannienion*, *i.e.* both the broad-leaved and coniferous woodlands of the North Patagonian region; by doing so, he thus added more "floristic content" to the order *Wintero-Nothofagetalia*, but maintained as nomenclatural type *Nothofagion betuloidis*, originating from the *Nothofagetum betuloidis* of Oberdorfer.

The syntaxonomic proposal of Pollmann (2001) would require the characteristic species of the new order to be the classic characteristic species of *Nothofago-Winterion*, likewise occurring in *Nothofagion betuloidis*. By contrast, the differential species of the suballiance *Weinmannienion* must be those that do not reach *Nothofagion betuloidis*. Thus our interpretation is as follows:

Characteristic species of *Wintero-Nothofagetalia betuloidis*: *Blechnum magellanicum, Desfontainia spinosa, Grammitis magellanica, Maytenus magellanica, Nothofagus nitida, Philesia magellanica, Pilgerodendron uviferum, Podocarpus nubigena, Polystichum multifidum, Tepualia stipularis.*

Characteristic species of *Nothofagion betuloidis*: *Berberis ilicifolia, Escallonia serrata, Lebetanthus myrsinites, Luzuriaga marginata, Nothofagus betuloides, Senecio acanthifolius.*

Differential species of *Weinmannienion trichospermae*: *Asteranthera ovata, Campsidium valdivianum, Fitzroya cupressoides, Griselinia ruscifolia, Lycopodium gayanum, Pernettya insana, Saxegothaea conspicua.*

This scheme would leave a floristic grouping, characteristic of the order, recognizable in Chile at least as far south as 50° 44' S, the latitude of the type relevé of *Nothofagetum betuloidis* [a relevé obtained by Skottsberg (1916), used by Oberdorfer (1960) in his original description, and lectotypified in Pollmann (2001)]. Impoverished forms of these evergreen Magellanic woodlands are found further south. Roig *et al.* (1985) classified these woodlands as *Embothrio-Nothofagion betuloidis*, in view of the presence of species of chamaephytic woodland substitution communities; however, we consider that these communities should be subordinated within *Nothofagion betuloidis*.

In addition, we consider that it is more appropriate to consider *Drimys andina* and *Myrceugenia chrysocarpa* as species of *Berberido trigonae-Nothofagetalia dombeyi*, since they mark the colder more continental nature of the North Patagonian woodlands, leading to floristic approximation to *Nothofagetea pumilionis* [see Eskuche (1999) and the reinterpretation of Pollmann (2001)]. Of course *Nothofagus dombeyi* and *Dasphyllum diacanthoides* should be considered characteristic of the class *Wintero-Nothofagetea*, but in Table II we have stressed the value of these species as discriminants within *Laurelio-Weinmannietum trichospermae* with respect to *Luzuriago-Nothofagetum nitidae*, in which neither species is present.

The first two columns of Table II clearly correspond to *Nothofagion betuloidis*. The last two columns (columns 21 and 22) were initially considered to fall into *Nothofago-Winterion* by their original authors, but fit better into *Myrceugenio-Nothofagion dombeyi* (*Berberido trigonae-Nothofagetalia dombeyi*). Pollmann (2001) has already proposed this solution for *Chrysosplenio-Nothofagetum dombeyi* (column 22), while the three relevés in column 21 should in our view be interpreted as belonging to this same association; thus the name *Nothofagetum dombeyi* Villagrán 1980, to which a number of relevés corresponding to *Fitroyetum cupressoidis* have also been assigned (Hildebrand-Vogel *et al.*, 1995), should be considered as a subsequent homonym and consequently rejected.

In our opinion, then, the new association *Luzuriago-Nothofagetum nitidae* is well delimited, and clearly enters into the alliance *Nothofago-Winterion*. Fortunately, the typical form, the *Tepualia stipularis*-variant and the subassociation *ugnetosum candollei* are all currently well-represented in diverse areas protected under the Chilean national conservation programme (SNASPE, Sistema Nacional de Areas Silvestres Protegidas por el Estado).

Acknowledgements - We thank the staff of the Instituto de Botánica of the Austral University of Valdivia for extensive help and support; the CONAF of the 10th Region and particularly the Castro and Valdivia units (notably Alex Rudloff) for logistic support in the course of fieldwork; Luis Gómez Orellana for the drawing in Fig. 7; and the University of Santiago for financing the stay of the Spanish authors in Chile.

Appendix 1: Phytosociological typology

Class *Wintero-Nothofagetea* Oberdorfer 1960
- Order *Laurelietalia philippianae* Oberdorfer 1960
  - Alliance *Nothofago-Eucryphion* Oberdorfer 1960
- Order *Wintero-Nothofagetalia* Roig, Dollenz & Méndez 1985
  - Alliance *Nothofago-Winterion* Oberdorfer 1960
    - Suballiance *Weinmannienion trichospermae* Oberdorfer 1960
      - Ass. *Laurelio philippianae-Weinmannietum trichospermae* Oberdorfer 1960 (*Saxegothaeo-Weinmannietum* Villagrán 1980 pro parte).
      - Ass. *Fitzroyetum cupressoidis* Oberdorfer 1960
      - Ass. *Pilgerodendronetum uviferi* Oberdorfer 1960
      - Ass. *Luzuriago polyphyllae- Nothofagetum nitidae* ass. nova
    - Suballiance *Laurelio philippianae-Nothofagenion dombeyi* Pollmann 2001
      - Ass. *Nothofagetum procerae* Oberdorfer ex Ramírez 1978
  - Alliance *Nothofagion betuloidis* (Oberdorfer 1960) Roig *et al.* 1985
    - Ass. *Nothofagetum betuloides* Oberdorfer 1960
- Order *Berberido trigonae-Nothofagetalia dombeyi* Pollmann 2001
  - Alliance *Myrceugenio-Nothofagion dombeyi* (Eskuche 1999) Pollmann 2001
    - Ass. *Chrysosplenio valdivici-Nothofagetum dombeyi* Oberdorfer 1960 prov.

REFERENCES

Alberdi M., C. Ramírez & L. Steubing, 1978.- La familia Hymenophyllaceae (Pteridophyta) en el fundo San Martín, Valdivia, Chile. II - Resistencia al desecamiento y sobrevivencia en comunidades antropogénicas. *Medio Ambiente*, **3** (2), 3-13.

Amigo J. & C. Ramírez, 1998.- A bioclimatic classification of Chile: woodland communities in the temperate zone. *Plant Ecol.*, **136**, 9-26.

Armesto J.J., J.C. Aravena, C. Villagrán, C. Pérez & G.G. Parker, 1996.- Bosques templados de la Cordillera de la Costa. *In*: *Ecología de los bosques nativos de Chile*. J.J. Armesto, C. Villagrán & M.T.K. Arroyo (eds.), Editorial Universitaria, 199-213.

Arroyo M.T.K., L. Cavieres, A. Peñaloza, M. Riveros & A.M. Faggi, 1996.- Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamérica. *In*: *Ecología de los bosques nativos de Chile*. J.J. Armesto, C. Villagrán & M.T.K. Arroyo (eds.), Editorial Universitaria, 71-99.

Braun-Blanquet J., 1979.- *Fitosociología. Bases para el estudio de las comunidades vegetales*. H. Blume Ediciones, 820 p.

Cabrera A.L. & A. Willink, 1973.- *Biogeografía de América Latina*. Secretaría General de la Organización de Estados Americanos, 117 p.

CONAF (Corporación Nacional Forestal), 1998.- *Experiencia silvicultural del bosque nativo de Chile. Recopilación de antecedentes para 57 especies arbóreas y evaluación de prácticas silviculturales*. Salesianos S.A., Santiago de Chile, 420 p.

Devall M.S., B.R. Parresol & J.J. Armesto, 1998.- Dendroecological analysis of a *Fitzroya cupressoides* and a *Nothofagus nitida* stand in the Cordillera Pelada, Chile. *Forest Ecol. Managem.*, **108**, 135-145.

Diem J. & J. Lichtenstein, 1959.- Las Himenofiláceas del área argentino-chilena del sud. *Darwiniana*, **11** (4), 611-760.

Donoso C., 1981.- Tipos forestales de los bosques nativos de Chile. *Corporación Nacional Forestal, Investigación y Desarrollo Forestal*, **38**, 1-70.

Donoso C., 1989.- Antecedentes básicos para la silvicultura del tipo forestal siempreverde. *Bosque*, **10** (1), 37-53

Donoso C., 1993.- *Bosques templados de Chile y Argentina. Variación, estructura y dinámica*. Editorial Universitaria, 484 p.

Donoso C. & J. Atienza, 1984.- Hibridación natural entre *Nothofagus betuloides* (Mirb.) Oerst. y *Nothofagus nitida* (Phil.) Krasser. *Medio Ambiente*, **7** (1), 9-16.

Donoso C., R. Grez & V. Sandoval, 1990.- Caracterización del tipo forestal alerce. *Bosque*, **11** (1), 21-34.

Eskuche U., 1968.- Fisionomía y sociología de los bosques de *Nothofagus dombeyi* en la región de Nahuel Huapi. *Vegetatio*, **16**, 192-204.

Eskuche U., 1999.- Estudios fitosociológicos en el norte de la Patagonia. II - Los bosques del *Nothofagion dombeyi*. *Phytocoenologia*, **29** (2), 177-252.

Fuenzalida H. & E. Pisano, 1965.- Biogeografía. *In*: *Geografía Eeonómica de Chile*, Texto refundido, CORFO (ed.), Santiago de Chile, 228-267

Gajardo R., 1994.- *La vegetación natural de Chile. Clasificación y distribución geográfica*. Editorial Universitaria, 165 p.

Géhu J.M. & S. Rivas-Martínez, 1981.- Notions fondamentaux de phytosociologie. *In*: *Syntaxonomie*. H. Dierschke (ed.), J. Cramer, Vaduz, 5-53.

Godley E.J., 1960.- The botany of southern Chile in relation to New Zealand and the Subantarctic. *Proc. Roy. Soc. London*, Ser. B, Biol. Sci., **152**, 457-475.

Gutiérrez R., 1984.- *Estudio comparativo de la redistribución de las precipitaciones entre rodales de los tipos forestales siempreverde y alerce*. Tesis Fac. Cien. Forest., Univ. Austral de Chile, 83 p.

Hauman M.L., 1913.- La forêt valdivienne et ses limites. *Recueil de l'Institut Botanique Leo Errera*, **IX**, 346-408. Bruxelles.

Hildebrand-Vogel R., 2002.- Structure and dynamics of southern Chilean natural forests with special reference to the relation of evergreen versus deciduous elements. *Folia Geobotanica*, **37**, 107-128.

Hildebrand-Vogel R., R. Godoy, A. Vogel & R. Carillo, 1995.- *Fitzroya cupressoides* (Mol.) Johnst. Primary forests of southern Chile - Flora, vegetation and mycorrhiza. *In*: *Applied Vegetation Ecology*. Y. Song, H. Dierschke & X. Wang, (eds.), Proc. 35th Symp. Intern. Ass. Veg. Sci., 1992, Shanghai, 108-121

Holdgate M.W., 1961.- Vegetation and soils in the South Chilean islands. *J. Ecol.*, **49**, 559-580.

Innes J.L., 1992.- Structure of evergreen temperate rain forest on the Taitao Peninsula, Southern Chile. *J. Biogeogr.*, **19**, 555-562.

Lusk Ch., 1995.- Seed size, stablishment sites and species coexistence in a Chilean rain forest. *J. Veg. Sci.*, 6, 249-256.

Lusk Ch., 1996.- Stand dynamics of shade-tolerant conifers *Podocarpus nubigena* and *Saxegothaea conspicua* in Chilean temperate rain forest. *J. Veg. Sci.*, 7, 549-558.

Lusk Ch., 1999.- Gradient analysis and disturbance history of temperate rain forest of the coast range summit plateau, Valdivia, Chile. *Rev. Chil. Hist. Nat.*, **69**, 401-411.

Marticorena C. & M. Quezada, 1985.- Catálogo de la flora vascular de Chile. *Gayana Bot.*, **42** (1-2), 5-157.

Marticorena C. & R. Rodríguez, 1995.- *Flora de Chile*. 1 - Pteridophyta-Gymnospermae. Universidad de Concepción, Editorial Anibal Pinto, 352 p.

Marticorena C. & R. Rodríguez, 2001.- Flora de Chile. 2 - Winteraceae-Ranunculaceae. Universidad de Concepción, Trama Impresores S.A., 99 p.

Matthei O., 1997.- Las especies del género *Chusquea* Kunth (Poaceae: Bambusoideae), que crecen en la X región, Chile. *Gayana Bot.*, **54** (2), 199-220.

McQueen D.R., 1976.- The ecology of *Nothofagus* and associated vegetation in South America. *Tuatara*, **22** (1), 38-68.

McQueen D.R., 1977.- The ecology of *Nothofagus* and associated vegetation in South America. *Tuatara*, **22** (3), 233-244.

M.O.P. (Ministerio de Obras Públicas), 1987.- *Balance Hídrico de Chile*. Dirección General de Aguas. Santiago de Chile. 23 p. + mapas.

Oberdorfer E., 1960.- Pflanzensoziologische studien in Chile. *Flora et Vegetatio Mundi*, **2**, 1-208.

Ogden J., G.H. Stewart & R.B. Allen, 1996.- Ecology of New Zealand *Nothofagus* forests. *In*: *The ecology and biogeography of* Nothofagus *forests*. T.T. Veblen, R.S. Hill & J. Read (eds.), Yale, 25-82.

Ormazábal C. & I. Benoit, 1987.- El estado de conservación del género *Nothofagus* en Chile. *Bosque*, **8** (2), 109-20.

Peralta M., 1975.- Tipificación de los principales suelos forestales del sector de la Cordillera de la Costa, entre el Cordón de Llancacura y el de Guayusca (40° 10' S y 73° 10' - 74° 00'). *Boletín Técnico Facultad de Ciencias Forestales, Universidad de Chile*, **31**, 1-50.

Pollmann W., 2001.- Caracterización florística y posición sintaxonómica de los bosques caducifolios de *Nothofagus alpina* (Poepp. et Endl.) Oerst.en el centro-sur de Chile. *Phytocoenologia*, **31** (3), 353-400.

Premoli A.C., 1996.- Leaf architecture of South American *Nothofagus* (Nothofagaceae) using traditional and new methods in morphometrics. *Bot. J. Linn. Soc.*, **121**, 25-40.

Ramírez C. & H. Figueroa, 1985.- Delimitación ecosociológica del bosque valdiviano (Chile) mediante análisis estadísticos multivariados. *Studia Oecologica*, **6**, 69-82.

Ramírez C. & H. Figueroa, 1987.- Fitosociología de los *Nothofagus* de la zona higromórfica chilena. *Bosque*, **8** (2), 127-132.

Ramírez C. & M. Riveros, 1975.- Los alerzales de Cordillera Pelada: flora y fitosociología. *Medio Ambiente*, **1** (1), 3-13.

Ramírez C., C. San Martín & R. Vásquez, 1996.- La vegetación potencial leñosa de la Cordillera Pelada (Valdivia, Chile). *Revista Geográfica de Valparaíso*, **26-27**, 233-250.

Ramírez C., L. Steubing & M. Alberdi, 1976.- La familia Hymenophyllaceae (Pteridophyta) en el Fundo San Martín, Valdivia, Chile. I - Taxonomía y ecología. *Medio Ambiente*, **2** (1), 21-28.

Reiche, K., 1907.- Grundzüge der Pflanzenverbreitung in Chile. *In*: *Die Vegetation der Erde*, **VIII**. A. Engler & O. Drude (eds.), Engelmann. Leipzig, 374 p.

Rivas-Martínez S., 1995.- Clasificación bioclimática de la Tierra (bioclimatical classification system of the world). *Folia Botanica Matritensis*, **16**, 1-25.

Rivas-Martínez S. & J. Loidi, 1999.- Bioclimatology of the Iberian Peninsula. *Itinera Geobotánica*, **13**, 41-47.

Rivas-Martínez S. & A. Penas, 1994.- *Clasificación biogeográfica y bioclimática de Sudamérica*. Comunicación al Congreso Latinoamericano de Botánica. Mar del Plata.

Riveros M. & C. Ramírez, 1978.- Fitocenosis epífitas de la asociación *Lapagerio-Aextoxiconetum* en el fundo San Martín (Valdivia, Chile). *Acta Cient. Venezolana*, **29**, 163-169.

Rodríguez R., 1995.- Pteridophyta. *In*: *Flora de Chile*, I. C. Marticorena & R. Rodríguez (eds.), Universidad de Concepción, 119-309.

Roig F.A., O. Dollenz & E. Méndez, 1985.- La vegetación de los canales, segunda parte. *In*: *Transecta botánica de la Patagonia austral*. O. Boelcke, D.M. Moore & F.A. Roig (eds.), Buenos Aires, 457-519.

Schmithüsen J., 1956.- Die räumliche Ordnung der chilenische Vegetation. *Bonner Geogr. Abh.*, 17, 1-89.

Schuhwerk F., 1986.- Kryptogamengemeinschaften in Waldassoziationen: ein methodischer Vorschlag zur Synthese. *Phytocoenologia*, 14 (1), 79-108.

Seibert P., 1979.- Die Vegetationskarte des Gebietes von El Bolson, Prov. Rio Negro, und ihre Anwendung in der Landnutzungsplanung. *Bonner Geogr. Abh.*, **62**, 1-96.

Skottsberg C., 1910.- Ubersicht über die wichtigsten Pflanzenformationen Sudamerikas s. von 41°, ihre geographischeVerbreitung und Beziehungen zum Klima. *Svenska Vet. Akad. Handl.*, **46** (3), 3-28.

Skottsberg C., 1916.- Botanische Ergebnisse der Schwedischen Expedition nach Patagonien und dem Feuerlanden 1907-1909. Die Vegetationsverhältnisse längs der Cordillera de los Andes S. 41° s. *Br. Svenska Vet. Akad. Handl.*, **56** (5), 1-366.

SPSS Inc., 2001.- *SPSS for Windows, v. 10.1.3*. Chicago, Illinois

Tomaselli R., 1981.- The longitudinal zoning of vegetation in the southern sector of the Andes. *Stud. Trent. Sci. Nat., Acta Biol.*, **58**, 471-484.

Van der Maarel E., 1979.- Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio*, **39**, 97-144.

Veblen T.T. & D.H. Ashton, 1982.- The regeneration status of *Fitzroya cupressoides* in the Cordillera Pelada, Chile. *Biol. Conserv.*, **23**, 141-161.

Veblen T.T., C. Donoso, T. Kitzberger & A.J. Rebertus, 1996.- Ecology of Southern Chilean and Argentinean *Nothofagus* forests. *In*: *The ecology and biogeography of* Nothofagus *forests*. T.T. Veblen, R.S. Hill & J. Read (eds.), Yale, 293-353.

Veblen T.T. & P.M. Schlegel, 1982.- Reseña ecológica de los bosques del sur de Chile. *Bosque*, 4 (2), 73-115.

Veblen T.T., P.M. Schlegel & J.V. Oltremari, 1983.- Temperate broad-leaved evergreen forests of South America. *In*: *Temperate broad-leaved evergreen forests*. Ovington (ed.), Elsevier Publishers, 5-31.

Villagrán C., 1980.- Vegetationsgeschichtliche und pflanzensoziologische Untersuchungen im Vincente Pérez Rosales Nationalpark (Chile). *Diss. Bot.*, **54**, 1-148.

Villagrán C., P. Moreno & R. Villa, 1996.- Antecedentes palinológicos acerca de la historia cuaternaria de los bosques chilenos. *In*: *Ecología de los bosques nativos de Chile*. J.J. Armesto, C. Villagrán & M.T.K. Arroyo (eds.), Editorial Universitaria, 51-69.

Weber H.E., J. Moravec & J.P. Theurillat, 2000.- International code of phytosociological nomenclature. 3rd edition. *J. Veg. Sci.*, **11**, 739-768.

Weinberger P., 1973.- Beziehungen zwischen mikroklimatischen Faktoren und natürlicher Verjungung araukano-patagonischer *Nothofagus*-Arten. *Flora*, **162**, 157-179.

Weinberger P., 1978.- Estudios sobre adaptación climática y las asociaciones de mirtáceas arauco-patagónicas. *Anales de Parques Nacionales*, **14**, 133-160.

Table I, Tableau I.- *Luzuriago polyphyllae-Nothofagetum nitidae* ass. nov.

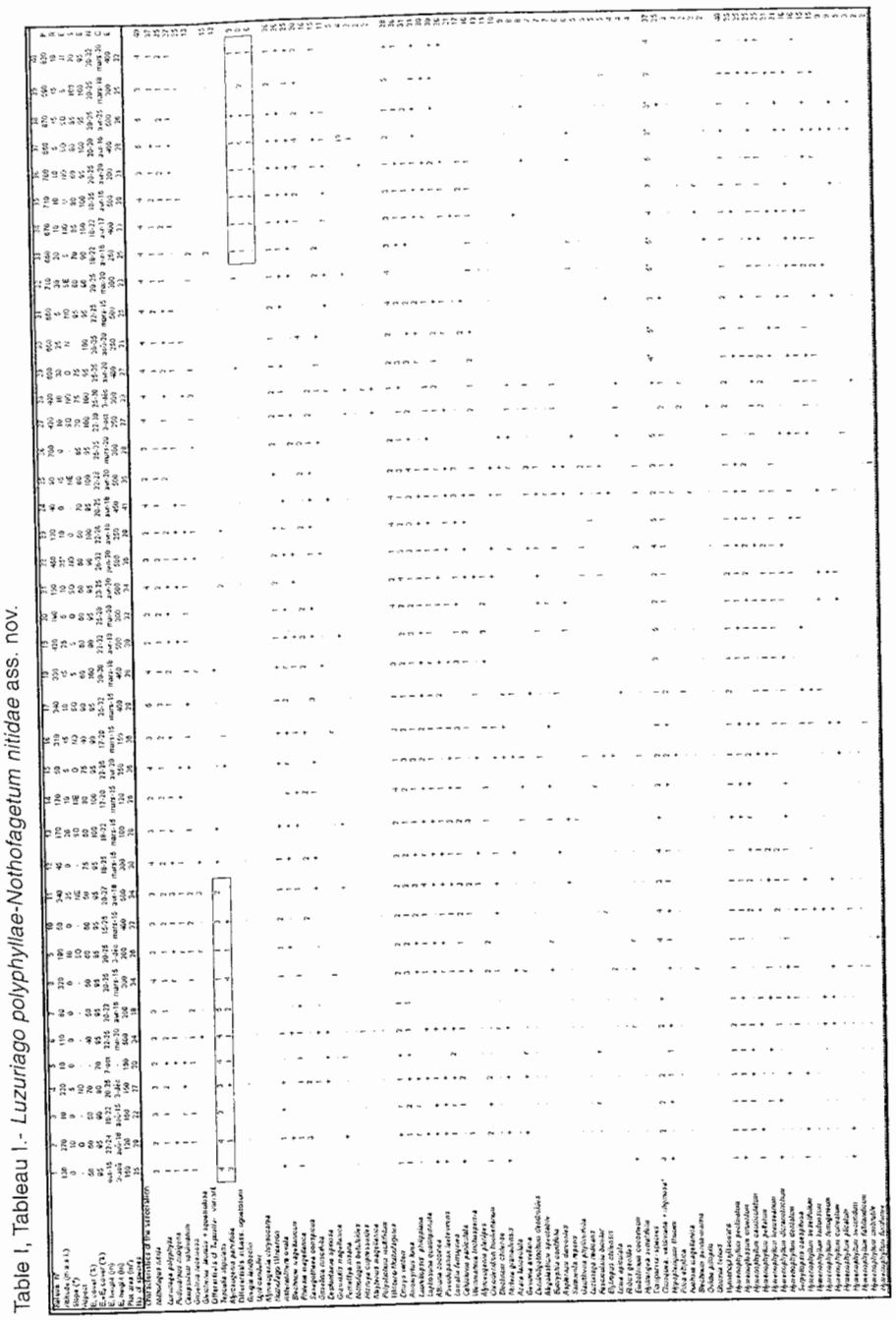


Table I - species present in only 1 relevé: *Amomyrtus meli* 1 in 20; *Berberis darwini* + in 26; *Blechnum corralense* + in 19; *Blechnum mochaenum* + in 15; *Ercilla syncarpellata* + in 25; *Hypolepis poeppigii* + in 6; *Lebetanthus myrsinites* 1 in 28; *Misodendron* sp. + in 38; *Polypodium feuillei* r in 29; *Pteris semiadnata* r in 22; *Ribes magellanicum* + in 27; *Uncinia* aff. *erinacea* r in 24; *Valeriana lapathifolia* + in 28.

Relevé locations (relevé n°, relevé code, province, precise locality, altitude, Southern latitude//Western longitude

1. 970118/1. Llanquihue. Alerce Andino National Park, sector Chaica. 130 m a.s.l. 41° 34' // 72° 34'
2. 970118/2. Llanquihue. Alerce Andino National Park, sector Chaica. Close to Lake Chaiquén. 275 m a.s.l. 41° 34' // 72° 33'
3. 970119/2. Chiloé. Chiloé National Park, sector Cucao. "El Tepual". 10 m a.s.l. 42° 36' // 74° 07'
4. 960130/7. Palena. South of Puente Quildaco, between Hualalhue and Contao. 220 m a.s.l. 41° 52' // 72° 41'
5. 970119/1. Chiloé. Chiloé National Park, sector Cucao. "El Tepual". 10 m a.s.l. 42° 36' // 74° 07'
6. 010125/2. Palena. Pumalín Park. Close to Lake Río Negro. 110 m a.s.l. 42° 42' // 72° 34'
7. 010126/2. Palena. Austral Road. Between Chaitén and Río Amarillo. 80 m a.s.l. 43° 00' // 72° 32'
8. 000123/2. Llanquihue. Between Correntoso and Lake Chapo. 320 m a.s.l. 41° 24' // 72° 38'
9. 960130/6. Palena. Hualalhue, westerly from Hornopirén. Close to Trafanco Bridge. 190 m a.s.l. 42° 00' // 72° 38'
10. 020127/1. Aysén. 30 kms road to Pto. Marín Balmaceda, from La Junta .50 m a.s.l. 43° 59' // 72° 43'
11. 010127/2. Palena. Pumalín Park. Ascending by Tronador Path. 340 m a.s.l. 42° 39' // 72° 35'
12. 020128/1. Aysén. 13 kms. road to Pto. Cisnes, from Austral road cross. 45 m a.s.l. 44° 41' // 72° 33'
13. 960130/8. Palena. Austral road southerly from Contao. 170 m a.s.l. 41° 49' // 72° 42'
14. 960129/1. Palena. Southerly from Contao, longer to Hornopirén. 175 m a.s.l. 41° 50' // 72° 41'
15. 010126/4. Palena. Austral road, northerly from Chaitén and Santa Bárbara. 55 m a.s.l. 42° 50' // 72° 47'
16. 000123/3. Llanquihue. Between (La Cascada) and Lake Sargazo. 310 m a.s.l. 41° 29' // 72° 38'
17. 020127/2. Aysén. Queulat National Park, sector Ventisquero Colgante; viewpoint height. 340 m a.s.l. 44° 27' // 72° 27'
18. 000123/4. Llanquihue. Alerce Andino National Park, Sector Sargazo. 330 m a.s.l. 41° 30' // 72° 37'. (HOLOTYPUS subas. typical)
19. 010204/1. Llanquihue. Alerce Andino National Park, Sector Sargazo. Along Lake Sargazo Path. 425 m a.s.l. 41° 30' // 72° 36'
20. 010122/1. Palena. Between Contao and Hornopirén, little northerly from Rio Cisne. 190 m a.s.l. 41° 57' // 72° 41'
21. 010123/1. Palena. Between Río Cisne and Hornopirén, close to Hualalhue cross. 190 m a.s.l. 41° 59' // 72° 40'
22. 010125/1. Palena. Pumalín Park. Close to Lake Tronador. 450 m a.s.l. 42° 39' // 72° 35'
23. 010125/3. Palena. Pumalín Park. Very close to Gral. Manuel Feliu's Bridge. 130 m a.s.l. 42° 40' // 72° 34'
24. 010126/3. Palena. Austral road. Northerly from Chaitén, between Chaitén and Santa Bárbara. 45 m a.s.l. 42° 53' // 72° 44'
25. 010127/1. Palena. Pumalín Park. Ascending by Las Cascadas Path. 90 m a.s.l. 42° 33' // 72° 37'
26. 000210/2. Valdivia. Puyehue National Park. Ascending to Antillanca, face to "mallín". 700 m a.s.l. 40° 46' // 72° 16'
27. 020128/2. Aysén. Queulat National Park, down to the south from Portezuelo. 420 m a.s.l. 44° 37' // 72° 26'
28. 020125/1. Aysén. Queulat National Park; going to the north just after Portezuelo. 490 m a.s.l. 44° 35' // 72° 26'
29. 010202/1. Chiloé. Chiloé National Park, Sector Abtao, Piuchué Range. 600 m a.s.l. 42° 23' // 73° 57'
30. 980218/4. Osorno. Osorno Coastal Range. Between Hueyusca and S. Pedro. 660m a.s.l. 40° 57' // 73° 40'
31. 020205/1. Osorno. Osorno Coastal Range; Hueyusca, above Los Cajones. 660 m a.s.l. 40° 52' // 73° 35'
32. 010203/1. Chiloé. Chiloé National Park, Sector Abtao, Piuchué Range 715 m a.s.l. 42° 23' // 74°

00'
33. 010203/2. Chiloé. Chiloé National Park, Sector Abtao, Piuchué Range. More easterly from relevé n° 32. 660 m a.s.l. 42° 23' // 73° 58'
34. 010213/1. Valdivia. Pelada Range, down to Hueicolla. 670 m a.s.l. 40° 10' // 73° 32'
35. 010213/2. Valdivia. Pelada Range, down to Hueicolla. 710 m a.s.l. 40° 10' // 73° 32'. (HOLOTYPUS subass.*ugnetosum candollei*)
36. 010213/3. Valdivia. Pelada Range, down to Hueicolla. 780 m a.s.l. 40° 09' // 73° 32'
37. 010213/4. Valdivia. Pelada Range, summit plateau easterly from the first Alerzal stand. 860 m a.s.l. 40° 10' // 73° 26'
38. 010213/5. Valdivia. Pelada Range, little northerly from Piedra del Indio. 870 m a.s.l. 40° 11' // 73° 25'
39. 000207/1. Valdivia. Valdivia National Reserve, close to CONAF guard's house. 590 m a.s.l. 40° 00' // 73° 22'
40. 020205/2. Osorno. Osorno Coastal Range; Huellelhue, at the summit plateau, "La Coigüería". 820 m a.s.l. 40° 47' // 73° 37'

Tableau II - References of the relevés ((shaded columns indicate tables that correspond to the original descriptions, and in which the type relevé is, or should be, included.).
1. *Nothofagetum betuloidis* (Oberdorfer, 1960, Table 30)
2. *Nothofagetum betuloidis* (Roig *et al.*, 1985, Tab. 44, cols. 54-56)
3. *Pilgerodendronetum uviferi* (Oberdorfer, 1960, Table 29)
4. *Luzuriago-Nothofagetum nitidae* subas. *nothofagetosum nitidae* (Table I present paper, relevés 12-32)
5. *Luzuriago-Nothofagetum nitidae Tepualia stipularis*-variant (Table I present paper, relevés 1-11)
6. *Luzuriago- Nothofagetum nitidae* subass. *ugnetosum candollei* (Table I present paper, relevés 33-40)
7. *Fitzroya* forest with *Nothofagus betuloides* and *N. nitida* (Hildebrand-Vogel *et al.*, 1995; Table 1, relevés 1-8, including relevés from Ramírez & Riveros (1975))
8. *Fitzroyetum cupressoidis* subass. *pilgerodendronetosum uviferi* (Tomaselli, 1981)
9. *Fitzroyetum cupressoidis* (Eskuche, 1968, Tab. 6d)
10. *Nothofago-Winterion* (Eskuche, 1968, Tab. 6b)
11. *Fitzroyetum cupressoidis* (Oberdorfer, 1960, Table 29)
12. *Fitzroya* forest with *Nothofagus dombeyi* (Hildebrand-Vogel *et al.*, 1995; Table 1, relevés 9-21, including relevés from Seibert (1979) and Villagrán (1980, Tab. 1: relevés 18, 61, 59, 85, 49))
13. *Laurelio-Weinmannietum trichospermae* subass. *luzuriagetosum polyphyllae* (Oberdorfer, 1960)
14. *Laurelio-Weinmannietum trichospermae* subass. *phylesietosum magellanicae* (Oberdorfer, 1960)
15. *Laurelio-Weinmannietum trichospermae* (Villagrán, 1980, Tab. 1: relevés 3, 17, 58, 65, 16, 71)
16. *Saxegothaeo-Weinmannietum trichospermae* (Villagrán, 1980, Tab. 1: relevés 66, 89, 210, 91, 90, 99, 207, 102)
17. *Nothofago-Winterion* (Eskuche, 1968, Tab. 6a)
18. *Laurelio-Weinmannietum trichospermae* (Eskuche, 1968, Tab. 6e)
19. *Nothofago-Winterion* (Eskuche, 1968, Tab. 6c)
20. *Nothofagetum procerae* (Pollmann, 2001, Tab. 2, col. 42)
21. *Nothofagetum dombeyi* (Villagrán, 1980, Tab. 1: relevés 84, 62, 70)
22. *Chrysosplenio valdivici-Nothofagetum dombeyi* (Oberdorfer, 1960, Table 28)

Table II.- Communities published as forming part of the alliance *Nothofago-Winterion*.
Tableau II.- Groupements publiés de l'alliance du *Nothofago-Winterion*.