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

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Abstract - A phytosociological study of the temperate rain forests dominated by Nothofagus nitida in Chile, one of the highest-collared woody species of temperate South America, indicated within the phytosociological concept of Nothofagus-Fractosperma forests, stands were found between the 44°48' and 46°47' South, in which these woodlands show highest floristic richness and a high number of species that occur only in this woodlands association. Fractosperma lindleyanum (Hook.) Hook. f. and Nothofagus nitida (Hook.) O. Kuntze are the typical species of the association.

Key words - systematics, forest communities, Fractosperma lindleyanum, Nothofagus nitida, Fractosperma lindleyanum-Nothofagus nitida association, biodiversity.

Résumé. Cette étude phytosociologique porte sur les forêts de Nothofagus nitida en Chilienne, l'un des arbres les plus élevés de l'Amérique du Sud tempérée. Les forêts de Nothofagus nitida ont été étudiées dans une largeur latitudinale de 44°48' à 46°47', où elle est dominée par un certain nombre d'espèces qui se rencontrent uniquement dans une association de Fractosperma lindleyanum (Hook.) Hook. f. et Nothofagus nitida (Hook.) O. Kuntze. Les forêts de Nothofagus nitida sont caractérisées par une grande diversité d'espèces et d'organismes.

CHAPTER 1: INTRODUCTION

Nothofagus nitida (Phil.) Kotschy is a broad-leaved evergreen tree species endemic to Chile. Its area of distribution extends from 30° 33' to 48° 30' S (Ornasalzal & Benoit, 1987), in the 16th and 17th regions (following the official nomenclature dividing Chile into 13 regions; see for example Marcioarena & Rodríguez, 1995). In its local name, "chiloé", reflects its broad-leaved character, shared with two other Chilean species, Nothofagus dombeyi (Hooker), the most widely distributed of the three, extending from 34° 31' to 48° 8' S, and Nothofagus betuloides (colhué Magallánico), which extends from 40° 3' 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 coexist overlap (Ornasalzal & Benoit, 1987), and of the three species it is the least tolerant of continentality. In other words, of the three species it is that which occurs at highest altitudes (McQueen, 1970) and thus the only one not found in Argentina. This biogeographical behavior may be related to a more ancestral phylogenetic position than N. dombeita and N. betuloides, as argued by Premoli (1996) on the basis of leaf architecture and allozyme 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 physiocoecological classifications as "Valdivian woodland" or "Valdivian rain forest" (Reiche, 1967; Skottsberg, 1910; Haunum, 1913), since for these authors the Valdivian territory extends from between 35° and 41° S to between 46° and 48° S. However, later geological studies such as Schmuthis (1956) and Oberdorfer (1960) indicate a subdivision of the wet temperate woodlands of southern Chile into three belts, not two, as recognized Valdivian, North Patagonian and Magallánico; this scheme offered a better account of the gradual north-to-south decline in fluvial 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 woodlands clearly outside the group defined as "Valdivian".

In subsequent non-physioecological studies that have proposed classification schemes for the Chilean temperate woodlands, authors have differed as to whether they recognize a category of woodland dominated by Nothofagus nitida. Firstly, Velten and Schlegel (1932) divided the woodlands of southern Chile into 23 types (1 deciduous and 20 predominantly evergreen, including coniferous). For the first time they established a forest type that was designated "Nothofagus nitida - Salmonocharas Pseudacacia nigra - Weimarvs", 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 designated "Evergreen Nothofagus - Weimarvs", which extends along the coastal belt, further south than the Nothofagus nitida type, and in which all three Nothofagus species may occur.

Secondly, Cisneros (1944) likewise presents a descriptive summary and additionally provides a cartographic representation of the vegetation units recognized throughout Chile. This author names one of his cartographic units "Bosque Laurisilva de Chiloé" ("Chiloé Laurelwood 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 nubigenus and Nothofagus nitida - Teupala stipulata.
II. STUDY AREA

The entire range in which Nothofagus nitida occurs falls within the Sub-Antarctic Province of the Antarctic Region biogeographic classification of Cabezas & Willink, 1973). The range largely corresponds to the Magellan District and the northernmost part of the Magellan District as defined by these authors (i.e. boundary at the 47th parallel). In terms of more recent biogeographic proposals, the range of Nothofagus nitida lies within the Valdivian Province of the Valdivian-Magellanic region (Rivas-Martínez & Penuelas, 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 Chacabuco 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 Pichache Range (isla Grande de Chiloé, heretofore 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 sites for acceptably natural Nothofagus nitida formations from the higher-altitude sites in the Pichache Range.

Zone B: A zone that we designate "Pedemóntes", including both the Andean foothills (generally of low altitude, not far from the sea, throughout the provinces of Llanquihue, Puerto Varas, 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 Teucrium stipulatum, from the foothills of the Pichache 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 isla Grande and Chichon Islands, comprising the fragmented territory of islands and peninsulas from the Guacalea 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 Guajardo 1994).

B. Climate

These three physiographic zones cover a large territory (6° latitude), but all show two climatic features that can be considered characteristic of Nothofagus nitida woodland: high temperature and very high rainfall (Fig. 2). Mean temperatures range from 12.2°C in
Valdivia (39° 48' S) to 71.7°C in Puerto Eden (49° 08' S), with thermal amplitude (i.e. difference between the mean temperatures of the coldest and hottest months) not exceeding 9.5°C (Arigo & Ramirez, 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; Ramirez et al., 1996), annual rainfall is more than 4000 mm (Ramirez & 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 (Gutiérrez, 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-hygrothermic, 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 Lodi (1999). Additionally, Nothofagus nitida woodlands may also occur in hyperthermic areas (12 ≤ Io ≤ 24), but in such cases Nothofagus nitida tends to seek edaphic compensation and associates with Tepualia stipularis in characteristic hygrophyllous 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 podzolic closer to the hill-top and in flatter areas (Peralta, 1975). Clearly podzolic soils with deficient drainage in flat hill-top sites are an ideal position for the Fitzroya cupressoides woodlands ("sabreras"), 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 sharply exceeds 800 m and where there is no clear altitudinal separation of Nothofagus nitida and Fitzroya cupressoides formations. Throughout zone A the predominance of soils is deep brownish acid soils with variable podzolation; the most extreme acidity and podzolation, in some cases reaching peat, is observed under the Fitzroya cupressoides formations in hill-top flat sites.

In zone B, the Andean Piedemontes, Nothofagus nitida woodlands are found on volcanic substrates ranging from trachybasalt to foid soils (Donoso, 1989), although in view of the hygrothermic nature of Nothofagus nitida it frequently occurs in soils with some degree of waterlogging and strong acidification of organic matter, typically in association with
There is little data available on the soils under woodlands in Zone C. Holdgate (1961) and Sim (1968) found that in the more northern parts of the island, the soils are generally sandy and shallow, with a thin layer of litter on top. The soil depth varies greatly from place to place, and is influenced by both the underlying geology and the amount of rainfall.

III. METHODOLOGY

A total of 40 relevés were obtained from woodland sites on the island as a whole. The samples were collected in the same area as the vegetation survey conducted by Fowke et al. (1991) and Buss (1992).

To avoid double sampling, we selected a single sample site from each of the 40 relevés. Each sample site was approximately 500 m² in size. The samples were collected at selected points in the woodland, and were then grouped into two categories: those that were located in the forest, and those that were located in the meadows.

For the characterization of structure, we used the following indices: number of stems per square meter, basal area per square meter, and mean height of the trees. The data were collected with a theodolite and a compass, and were recorded on 1:25000 scale maps.

IV. RESULTS

The results of the vegetation survey are shown in Table 1. The table shows the number of species, the number of individuals, and the percentage of each species in the total number of individuals. The data show that the woodland sites are dominated by a few species, such as Eucalyptus gunnii and Casuarina equisetifolia, which together account for more than 50% of the total number of individuals.

A floristic composition

Table 1 shows the floristic composition of the woodland sites. The data show that the woodland sites are dominated by a few species, such as Eucalyptus gunnii and Casuarina equisetifolia, which together account for more than 50% of the total number of individuals.
other Chilean temperate rainforest. Figure 3 summarizes the life-form composition of the floristic groupings detailed in Table I. The life-form distributions are based on Holderegger-Vogel (2002), who catalogues more than 100 species of the flora of the temperate woodlands of southern Chile; however, we have included an additional category, "epiphytic chamaephyte," for strictly epiphytic forms such as the cryptogams/lichens, which are abundant in these communities.

The main grouping in Table I (relevé 1-22) represents what we consider to be Luehmannia polyphylla-Winteria nitidae subass. nothofagidum nitidae subass. nova (holotype relevé n° 18, Table I), which occurs practically throughout our study area. However, none of these relevés (n° 1-11, Table I) are representative of a specific situation arising on contact between Luxurago-Nothofagus nitidae and formations dominated by trigo (the myrtaceous *Epacris stipulata*), which occur in locations with geologically waterlogging, generally in flat valley bottoms. When topography is favourable the area of contact is sufficiently extensive for development of edaphophilous woodland in which *Nothofagus nitida* dominates the upper stratum but in which cover tends to be lower (50-60%). This community, although it is frequent and occupies considerable areas, is clearly transitional between Luxurago-Nothofagus nitidae and woodlands with edaphically determined distributions (such as *Pilgerodendron uvifera*) although we cannot rule out the possible existence of a new community identifiable as "Epacris stipulata". In such transitional situations, the most suitable taxonomic rank is probably that of variant, i.e. *Luxurago-Nothofagus Epacris stipulata* 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 Pichilemu Range on Chiloé Island in the south. These tend to be formations totally dominated by *Nothofagus nitida*, with an understory containing certain species absent from low-altitude relevés or relevés obtained at some distance from the coast; these include the myrtaceous *Ugni condollei*, as well as *Grevia landbeckii* and less frequently *Menisperma chrysocarpa*. We propose classifying this community as a subassociation *Luxurago-Nothofagus nitidae robusta*, *epacrisym candelae subass. nova* (holotype relevé n° 35, Table I).

A key problem in the identification of this new association is that its bioclimatic, eutal and floristic position overlaps with that of three other associations of the *Nothofagus Winteri* ar alliance: *Luehmannia-Winteria nitidae*, *Pillarodendron uvifera* and *Pilgerodendron uvifera*. 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 summarises known published relevés for the associations of this type originally described in the *Nothofagus Winteri* association. The table thus includes two associations dominated by other collules, namely *Chrysoxylon-Nothofagus donkeyi* and *Nothofagus betuloides*, though note that it has recently been proposed that the former be included in a different order (Pollmann, 2001).

**B. Structures of the *Nothofagus nitida* woodlands**

**Stress and species**

The general appearance of the *Luxurago polyphylla-Nothofagus nitidae* is that of a rather closed canopy, more homogeneous with increasing dominance of *Nothofagus nitida* in the lower stratum. In general, *Nothofagus nitida* shares dominance with individuals of
Fig. 4. Ranges for all species (E, dotted bars) and subdominant species (E, dark bars) in each of the 40 relevés from Table 1.

Table 1. - Dendrometric data (diameter at breast height, DBH, cm, and basal area, BA, m²) in three selected plots. N = no. of individuals of each species with DBH > 10 cm, minimum (DBHmin) and maximum (DBHmax) DBH values in each plot are also shown. BA was calculated as π(DBH²/4).

<table>
<thead>
<tr>
<th>Species</th>
<th>Plot 1 (min. 21, 14, 21)</th>
<th>Plot 2 (min. 1, 13, 21)</th>
<th>Plot 3 (min. 14, 17, 21)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>DBH (min., max.)</td>
<td>BA (min., max.)</td>
</tr>
<tr>
<td>D. nigra</td>
<td>17</td>
<td>10.3 - 16.4</td>
<td>10.9 - 20.3</td>
</tr>
<tr>
<td>L. philippiana</td>
<td>11</td>
<td>10.2 - 16.4</td>
<td>10.9 - 20.3</td>
</tr>
<tr>
<td>Callicarpa simonii</td>
<td>1</td>
<td>10.3 - 10.3</td>
<td>10.9 - 10.9</td>
</tr>
<tr>
<td>Lagerstroemia speciosa</td>
<td>1</td>
<td>19.8 - 19.8</td>
<td>10.9 - 19.8</td>
</tr>
<tr>
<td>Salix fragilis</td>
<td>1</td>
<td>19.8 - 19.8</td>
<td>10.9 - 19.8</td>
</tr>
<tr>
<td>N. ruthagarica</td>
<td>20</td>
<td>13.6 - 19.6</td>
<td>11.2 - 21.4</td>
</tr>
<tr>
<td><em>Total</em> (min. 50, 21, 21)</td>
<td>598</td>
<td>4.37</td>
<td>7.17</td>
</tr>
</tbody>
</table>
tated a maximum value of 160 m² ha⁻¹ for mixed Nothofagus woodland in southern Chile, while Ogden et al. (1996) reported 150 m² ha⁻¹ for Nothofagus woodlands with or without conifers in New Zealand.

**Understory**

Although we have not performed a quantitative survey of seedling and sapling presence, we observed and annotated the regeneration of tree species in the understory. Clearly important species are *Drimus winteri*, *Laurinolax philippiana*, *Anomamyrs nova* and *Callophyles paniculatus*, 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 faginea* (92%), *Sigirepiazza conspicua* (90%) and *Podocarpus lambgina* (60%). *Nothofagus miltii* was detected in the understory layer in only 33% of relevés, but this figure may be misleading as it is a 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 miltii* 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 understory, together with the strongly ombrophilous nature of *Laurinolax philippiana - Nothofagus miltii*, is a key factor in the interior of these woodlands, which usually have rather dense shrub and epiphyte flora, as well as humid and fully forest cover. The synusia formed by these forms is particularly important as woodlands of this type, in which they 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 *nothofagus miltii* are mostly grouped together (branch A-2), and within this branch nearly all of the relevés of the hypophyllous *Tsuga - stipularis - variabilis* (relevés 1-9) are grouped into a discrete category (branch A-2b).

Secondly, four relevés of the subassociation *nothofagus miltii* are grouped apart from the rest and together with those of subassociation *apetinum 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 subassociation *apetinum candollei*. In fact relevés 29 and 32 include *Gregoria 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 *Laurinolax - Nothofagus*, and in fact rather closer to that of *Nothofagus beecheyi*, which replaces *Laurinolax - Nothofagus* in this National Park between about 500 m and the tree limit.
A. Phytogeographic aspects

Since *Nothofagus nitida* is a Chilean endemic, the new association described here is likewise endemic. This association has been detected at least 44° to 48° S, at the level of Puerto Chacabuco, but previous reports suggest that it may occur even further south (for example the woodlands studied by Imbesi 1932 in the Tanco Peninsula very close to 46° 30' S).

However, although *Nothofagus nitida* extends as far south as the 48th parallel, it is still not possible to precisely evaluate how much area might be occupied by these *Larrea-nothofagustum woodlands, and how much it now by woodlands in which both colute species of this region are present (*N. betuloides* and *N. nitida*). Communities of the latter type should be interpreted as *Nothofagustum betuloides*, in view of the floristic composition of this association as originally described. For Donoso (1993), all of the oceanic territory corresponding to that here demarcated the Aysén channels zone from the 47th parallel southwards the Magallanes Coahu 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 in line with previous reports: see for example McGuire'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 *Larrea-Nothofagustum nitidae* are woodlands requiring very high rainfall, though in relatively low-rainfall areas "hydrophytic 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 (1968), who studied woodlands on fluvial terraces of the lowest altitudinal belt, at the mouth of the river Chesa in the north of Chiloé island. Godley (1960) noted that this characteristic of *Nothofagus nitida* constitutes an ecological separation from the Valdivian woodland ("Eucryphia-Larrea-Weinmannia forest") present in this territory, since this latter occurs well-drained slopes while *Nothofagus nitida* grows on more acid and less well-drained soils. Both *Tepualia stipularis* and *Myrceugenia perryi*ia are good indicators of the degree to which gleyation occurs in the arid woodland we denominates *Larrea-Nothofagustum, Tepualia stipularis*-variant. Weinberger (1978) notes these two myrtacées as the most hydrophilous of those occurring in Chile, and likewise the most dependent on high atmospheric humidity.

The optimal position for *Larrea-Nothofagustum nitidae*, in terms of the bioclimatic classification of Rivas-Martínez (1995), is in the upper sub-belt of the Mesotemperate belt, extending into the Subarctis. As regards rainfall, the optimal position is the Ultrahygrothermal belt (Amigo & Ramírez, 1988). 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 dries places...
Nothofagus nitida at a disadvantage with respect to *N. dombyi*, so that in the zone we denominated Podomantes *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. dombyi*, in pure stands or in association with *Laurelo-Quilmesietum* (see Fig. 7).

Extremely peaty soils are not favourable for *Laurelo-Nothofagetae nitidae*. In such situations it is generally replaced by communities dominated by the heathies *Eucalyptus cypresses*, *Fitzroya cupressoides* and *Piptospermaeformis*. Clearly, transitional environments often occur between poorly drained soils with more or less prolonged waterlogging (which, as noted, are acceptable for *Laurelo-Nothofagetae nitidae*) and peaty soils showing classic histosol characteristics and the presence of differentiated species of the class *Myrtico-Sphagnieta*: in such transitional environments, attempts at phytosociological classification on the basis of the dominant tree are likely to be unsuitable. An example of a community intermediate between *Laurelo-Nothofagetae nitidae* and *Fitzroyetum*

cupressoides was reported by Donoso et al. (1990) under the denomination "Alceo-Chiloe Cupress forest subtype" (see comments below in Section D Syntaxonomic aspects).

In areas with marked oceanic influx, such as the south of Chiloé island, formations classified as *Pilgerodendron uviferum* are frequent, and the constant presence of *Tepualia stipularis* in these formations has meant that they are referred to by the vernacular name *tepuali*. Yebbel et al. (1983), in their forest type no 5, reported tepualies present in sites in southern Chile adjacent to *Nothofagus nitida* woodlands in positions with better drainage. This description appears to propose the community which we denominate *Laurelo-Nothofagetae*, *Tepualia stipularis-variato*.

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

A good example of the way in which these two associations separate is shown in Fig. 7, corresponding to the surroundings of lake Rio Negro (42° 42' S, see Fig. 1): this is a flat-bottomed valley with east-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/Laurelo-Nothofagetae* sequence down the slope on the west side; the *Fitzroyetum* woodland is abundant on the very rainy hilltops, and descends some distance down-slope along streambanks with high soil moisture content. At lower levels the topography and rainshadow allow patches of *Laurelo-Nothofagetae* to grow on slopes otherwise largely covered by *Laurelo-Quilmesietum*. In addition, it can be seen 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 colonised by *Laurelo-Nothofagetae*, while the hill slopes and valley bottoms (receiving lower rainfall) are occupied by *Laurelo-Quilmesietum*. 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-variato* of *Laurelo-Nothofagetae*.

C. Filmy ferns

Detailed data indicating which Chiloé rainforest communities are richest in hymenophyllaceae are not yet available. However, he bioecologic position and territorial range of *Laurelo-Nothofagetae 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 (Rodriguez, 1995). Three of these species are endemic to the Juan Fernandez 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 *Laurelo-Nothofagus* communities is highest in the various forms of *Laurelo-Nothofagus nitidae* and is otherwise approached only in *Laurelo-Quilmesietum subhirsutum* and *Laurelo-Quilmesietum polyphyllaeum* (described as the most Alyceae form of this association). The fact that these are the only communities within the alliance that may contain species like *Hymenophyllum crebescens* or *Hymenophyllum caudiculatum* constitutes an additional argument in favour of the oceanic
Les caractéristiques des communautés de Luzula-Lyoniaëtum ont été étudiées dans le cadre d'une recherche sur l'écologie des forêts de la région. Les auteurs ont observé que les communautés de Luzula-Lyoniaëtum sont caractérisées par une forte diversité végétale, avec une dominance de la luzule et des plantes de la famille des Ericaceae. Les communautés de Luzula-Lyoniaëtum sont généralement associées à un sol humide et acide, avec une faible Richesse en eau et une haute Richesse en azote. Les communautés de Luzula-Lyoniaëtum sont également caractérisées par une forte Richesse en biodiversité, avec une grande diversité de spéces végétales et animales. Les communautés de Luzula-Lyoniaëtum sont également caractérisées par une forte résilience écologique, avec une capacité à se rétablir rapidement après un perturbateur.
II we have stressed the value of these species as discriminants within Laurisilva-Winnemaniae trichospermae with respect to Lusciniae-Nothofagetea nitidae, in which neither species is present.

The first two columns of Table II clearly correspond to Nothofagetea bivalvidae. The last two columns (columns 21 and 22) were initially considered to fall into Nothofagetea-Winnemaniae by their original authors, but fit better into Myrceugenia-Nothofagetea bivalvidae (Bergen et al., 1985). Pollmann (2001) has already proposed this solution for Cyrtomiuminae-Nothofagetea bivalvidae (column 22), while the three relevés in column 21 should in our view be interpreted as belonging to this same association; thus the name Nothofagetea bivalvidae Villagrán 1990, to which a number of relevés corresponding to Fitzroya cupressoides have also been assigned (Hillerbrand-Vogt et al., 1995), should be considered as a nomenclatural homonym and consequently rejected.

In our opinion, the new association Luscinia-Nothofagetea nitidae is well-delineated, and clearly enters into the alliance Nothofagetea-Winnemaniae. Fortunately, the typical form, the Tequilla stipularis-variet petraeana subassociation arenariae 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).

Acknowledgments - We thank the staff of the Instituto de Biología of the University of Chile for extensive help and support; the CONAF of the 10th Region and particularly for the Castro and Valdivia units (Sergio A. Hudebo for logistic support in the course of fieldwork). Luc Iván Créven for the drawing in Fig. 7, and the University of Santiago for financing the stay of the Spanish authors in Chile.

Appendix 1: Phytoecological typeology

Class: Winnemaniae-Nothofagetea Oberdorfer 1960
Order: Laurisilva philippinicae Oberdorfer 1966

Alliance Nothofagetea-Eucalyptus Oberdorfer 1960

Order: Winnemaniae-Nitidae Oberdorfer 1960

Suballiance Winnemaniae trichospermae Oberdorfer 1960


Ass. Fitzroya cupressoides Oberdorfer 1960

Alliance: Subassociation arecae Oberdorfer 1960

Subassociation Laurisilva philippinicae-Nothofagetea nitidae Pollmann 2001

Ass. Nothofagetea nitidae Oberdorfer ex Ramirez 1978

Alliance: Nothofagetea-Bivalvidae Oberdorfer 1960 (Koeg et al., 1985)

Subassociation bivalvidae Oberdorfer 1960

Order: Bergeniae-Myrceugeniae 1985

Subassociation: Bergeniae-Myrceugeniae 1985


This scheme would leave a floristic grouping, characteristic of the order, recognizable in Chile at least as far south as 59° 44'S, the latitude of the type relevé of Nothofagetea bivalvidae (a relevé obtained by Skuneberg, 1916), used by Oberdorfer (1960) in his original description, and recognized in Pollmann (2001). Impoverished forms of these evergreen Magellanic woodlands are found further south. Koeg et al. (1985) classified these woodlands as Embryophyta-Winnemaniae, in view of the presence of species of shrub-like woodland substrate communities; however, we consider that these communities should be subordinated within woodlands bivalvidae.

In addition, we consider that is more appropriate to consider Drimys andina and Myrceugenia chrysocarpa as species of Bergeniae-Myrceugeniae bivalvidae, since they mark the colder more continental nature of the North Patagonian woodlands, leading to floristic affinities to Nothofagetea puniculatae (see Esbeticz (1999) and the reinterpretation of Pollmann (2001)). Of course Nothofagetea nitidae and Drimys andina should be considered characteristic of the class Winnemaniae-Nothofagetea, but in Table

Diospyros magellanicae, irregularly present in Laurisilva-Winnemaniae nitidae.

A different question is to which order Laurisilva-Nothofagetea nitidae (and its alliance Nothofagetea-Winnemaniae) should be assigned. Originally, Oberdorfer (1960) recognized two suballiances within Nothofagetea-Winnemaniae, Winnemaniae strigillospermae und Winnemaniae nitidae, this latter including only Nothofagetea nitidae, but the alliance was maintained within the order Laurisilva-Winnemaniae. In a later study of Magellanic woodlands, Roeg et al. (1985) offered a more diversified classification of the evergreen woodlands, recognizing two alliances, Embryophyta-Nothofagetea nitidae and Nothofagetea bivalvidae; at the same time they defined a new order including both alliances, denominated Winnemaniae-Nothofagetea nitidae. Finally, Pollmann (2001) adopted the new order proposed by Roeg et al. (1985), but included within it all the associations of Winnemaniae nitidae, 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 Winnemaniae-Nothofagetea nitidae, but maintained as nomenclatural type Nothofagetea nitidae, originating from the Nothofagetea nitidae of Oberdorfer.

The taxonomic proposal of Pollmann (2001) would require the characteristic species of the new order to be the classic characteristic species of Nothofagetea-Winnemaniae, likewise occurring in Nothofagetea bivalvidae. By contrast, the differential species of the suballiance Winnemaniae nitidae must be those that do not reach Nothofagetea nitidae. Thus our interpretation is as follows:

Characteristics species of Winnemaniae nitidae: Beeflora magellanicae, Drimys andina, Grammitis magellanicae, Magellanes magellanicae, Nothofagetea nitidae, Polystichum nitidum, Polystichum nitidum, Polystichum nitidum, Pseudocatopsis nitidae, Senecio azacrii-

diosae.

Differential species of Winnemaniae nitidae: Austinothera ovata, Campsidiun nitidum, Fitzroya cupressoides, Giraldia nitidum, Licopus podophyllum, Pernettya nitidae, Sorothea nitidae.

This scheme would leave a floristic grouping, characteristic of the order, recognizable in Chile at least as far south as 59° 44'S, the latitude of the type relevé of Nothofagetea bivalvidae (a relevé obtained by Skuneberg, 1916), used by Oberdorfer (1960) in his original description, and recognized in Pollmann (2001). Impoverished forms of these evergreen Magellanic woodlands are found further south. Roeg et al. (1985) classified these woodlands as Embryophyta-Winnemaniae, in view of the presence of species of chamaephytic woodland substrate communities; however, we consider that these communities should be subordinated within woodlands bivalvidae.

In addition, we consider that it is more appropriate to consider Drimys andina and Myrceugenia chrysocarpa as species of Bergeniae-Myrceugeniae bivalvidae, since they mark the colder more continental nature of the North Patagonian woodlands, leading to floristic affinities to Nothofagetea puniculatae (see Esbeticz (1999) and the reinterpretation of Pollmann (2001)). Of course Nothofagetea nitidae and Drimys andina should be considered characteristic of the class Winnemaniae-Nothofagetea, but in Table

Historically Nothofagus erectus, but both contain Nothofagus dombei with high constancy, and both lack X. nitida as well as the other species we have selected as differentials in Table II (Gleichenio-Griffitho-Fulgevallia). To these we may add

Diospyros magellanicae, irregularly present in Laurisilva-Winnemaniae nitidae.
<table>
<thead>
<tr>
<th>Line</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>L. longifolium, Alpine Aconite National Park, sector Chica. 130 m a.s.l. 41°34' 70°34'</td>
</tr>
<tr>
<td>2</td>
<td>L. longifolium, Alpine Aconite National Park, sector Chica. Close to Lake Chaquiu. 273 m a.s.l. 41°34' 70°33'</td>
</tr>
<tr>
<td>3</td>
<td>Chiloé, Chiloé National Park, sector Cacai. &quot;El Topo&quot;. 10 m a.s.l. 42°36' 70°07'</td>
</tr>
<tr>
<td>4</td>
<td>L. longifolium, South of Punta Quilico, between Hualma and Comata. 220 m a.s.l. 44°52' 72°31'</td>
</tr>
<tr>
<td>5</td>
<td>L. longifolium, Chiloé, Chiloé National Park, sector Cacai. &quot;El Topo&quot;. 10 m a.s.l. 42°36' 70°07'</td>
</tr>
<tr>
<td>6</td>
<td>Palena, Pamalín Pk. Close to Lake Río Negro. 110 m a.s.l. 42°42' 72°35'</td>
</tr>
<tr>
<td>7</td>
<td>Palena, Atacama Road. Between Chaitén and Rio Artillería. 89 m a.s.l. 42°00' 72°32'</td>
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<tr>
<td>8</td>
<td>L. longifolium, Between Corrales and Lake Chaquiu. 320 m a.s.l. 44°24' 72°35'</td>
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<tr>
<td>9</td>
<td>Palena, Hualma, westerly from Hualma. Close to Tedesco Bridge. 190 m a.s.l. 42°00' 72°38'</td>
</tr>
<tr>
<td>10</td>
<td>Palena. 30 km road to Pro. Malín Bovida, from La Junta. 50 m a.s.l. 43°59' 72°35'</td>
</tr>
<tr>
<td>11</td>
<td>Palena. Pamalín Park. Ascending by Transito Pass. 340 m a.s.l. 42°59' 72°35'</td>
</tr>
<tr>
<td>12</td>
<td>Palena. 13 km road to Pro. Cristo, from Austral road-pass. 45 m a.s.l. 44°41' 72°12'</td>
</tr>
<tr>
<td>13</td>
<td>Palena. Austral road westerly from Comata. 170 m a.s.l. 41°49' 72°42'</td>
</tr>
<tr>
<td>14</td>
<td>Palena. Southernly from Comata, longer, is Hualma. 175 m a.s.l. 41°15' 72°41'</td>
</tr>
<tr>
<td>15</td>
<td>Palena. Austral road, northerly from Chaitén and Santa Barbara. 55 m a.s.l. 42°50' 72°47'</td>
</tr>
<tr>
<td>16</td>
<td>L. longifolium, Between (L. Cascada) and Lake Sagarra. 310 m a.s.l. 44°29' 72°35'</td>
</tr>
<tr>
<td>17</td>
<td>Palena. Queral National Park, sector Ventagno Colgante, viewpoint height. 340 m a.s.l. 44°27' 72°27'</td>
</tr>
<tr>
<td>18</td>
<td>L. longifolium, Alvarado Aconite National Park, Sector Sagarra. 330 m a.s.l. 44°30' 72°37'</td>
</tr>
<tr>
<td>19</td>
<td>L. longifolium, Alvarado Aconite National Park, Sector Sagarra. Along Lake Sagarra Path. 425 m a.s.l. 44°30' 72°36'</td>
</tr>
<tr>
<td>20</td>
<td>Palena. Between Comata and Hualma, little northerly from Rio Cristo. 190 m a.s.l. 44°57' 72°41'</td>
</tr>
</tbody>
</table>

Table 1: Species present in only 1 relevé: Anemone nemorosa in 20, Berberis darwinii in 26, Betula campestris in 19, Betula mendocina in 15, Erythronium revolutum in 23, Hypephyllum pusillum in 6, Leptocarpus unifoliatus in 1, 28, Meliosma sp. in 38, Nepeta densiflora in 29, Poa annuina in 21, Ribes megapotanicum in 27, Uncinia arenaria in 24. All relevés located (refer to 3), relevé code, Province, precise location, altitude, Southern latitude/Western longitude.