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THE SUBANTARCTIC *NOTHOFAGUS* FORESTS OF TIERRA DEL FUEGO: DISTRIBUTION, STRUCTURE AND PRODUCTION

EMILIA GUTIÉRREZ[1], V. RAMÓN VALLEJO[2] , JOAN ROMAÑÀ[2] & JAUME FONS[2]

[1] Departament d'Ecologia. Facultat de Biologia. Universitat de Barcelona. Av. Diagonal, 645. 08028 Barcelona. Spain.
[2] Departament de Biologia Vegetal. Facultat de Biologia. Universitat de Barcelona. Av. Diagonal, 645. 08028 Barcelona. Spain.

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SUMMARY

Evergreen *Nothofagus betuloides* and deciduous *N. pumilio* form the main forest types in Tierra del Fuego. These forests were sampled along two altitudinal gradients to study their structure and dynamics and assess the causes of their distribution.

The distribution patterns of the two species of *Nothofagus* seem to respond to different climates and soils. The dominant soil processes are hydromorphy in the evergreen forest and podzolization in the deciduous one. *N. betuloides* is an evergreen resilient to short-term environmental fluctuations, due to its ability to retain nutrients. Leaves on the tree may last up to 7 years, with an average density of 17 mg cm^{-2}. In contrast, the leaves of *N. pumilio* are shed in autumn and reach only 8 mg cm^{-2}.

In both types of forests the following features can be outlined. Old-growth forest stands develop in the middle and lower slopes. The distribution of diameter sizes of the trees usually shows a pronounced bimodality. Recruitment is discontinuous as shown by the spatial pattern of tree sizes, and regeneration is vegetative in the upper slopes.

Leaf area indices range between 2.3 and 2.8 m^2 m^{-2} for the deciduous forest and from 2.5 to 4.5 m^2 m^{-2} for the evergreen forest. It appears that tree standing biomass ranges between 6.0 and 13.6 kg C m^{-2} in the deciduous forest, and between 10.5 and 15.6 Kg C m^{-2} in the evergreen forest. Production varies from 148.0 to 372.1 g C m^{-2} yr^{-1}, and from 204.6 to 346.4 g C m^{-2} yr^{-1}, respectively. In relation to boreal forests, biomass can be considered high, but production is medium to low. The relation of wood production to leaf biomass shows that *N. betuloides* behaves similar to coniferous forests and *N. pumilio* as hardwood forests.

There is much accumulation of organic matter on the forest floor, especially coarse wood debris, reflecting the stage of development of these forests and the unfavourable conditions for litter decomposition.

KEY WORDS: *Nothofagus*, production, forest structure, regeneration, forest soils, Tierra del Fuego.

INTRODUCTION

The forests of Tierra del Fuego extend along the southernmost foothills of the Andes, between 53° 30' and 56° South (Fig. 1). They are formed by three broad-leaved species of *Nothofagus*. *N. betuloides* (Mirb.) Oerst. is the main constituent of the evergreen Magellanic forest, whereas *N. pumilio* (Poepp. and Endl.) Krasser forms the deciduous forest. The third species, *N. antarctica* (Forstf.) Oerst., also deciduous, is restricted to the least favourable habitats. The forest ecosystems of Tierra del Fuego are poorly known, with the possible exception of their floral composition. Geographical location and climate have both contributed to this lack of studies, even though peculiar environmental conditions make this region a place of considerable scientific interest. It is the closest area to the South Pole not covered by ice. The influence of the Andes, Quaternary glaciations and the nature of the substrate formed mainly by metamorphic and volcanic rocks, have shaped a unique landscape.

Tierra del Fuego is a group of islands to the south of the Magellan Straits, and only 1,170 km from Antarctica. The disjunctive distribution of living *Nothofagus* attests to an ancient trans-Antarctic forest belt. Nowadays, the proximity to this continent is reflected in the climate, which is much colder than that of the Northern Hemisphere at the same latitude. The climate is cold-temperate without pronounced thermal oscillations during the year.

Measurements taken at Ushuaia, representative of the forest area, show an average temperature of 9.4 °C in summer and 1.7 °C in winter (Fig 2). Thus, the average annual variation is less than 8 °C. Strong winds are the other climatic characteristic of the zone. Climatic subzones are caused by the mountains of the Andes, which in Tierra del Fuego change direction and run from west to east, bordering the western and southern coasts.

The Andes, as in the rest of the South American continent, are the great structural element of the landscape. The distribution and type of ecosystems are, to a great extent, determined by the presence, arrangement and elevation of the mountains, which were lifted in the Pliocene. The altitude of the Andes in Tierra del Fuego is not great, yet sufficient to slow down the clouds from the Pacific ocean.

Gradual precipitation has created a gradient ending in steppes. Consequently, the coastal strip occupied by evergreen forest has a cold-temperate climate with high humidity (Cfk'c, according to the Koppen classification; PISANO, 1981). The area occupied by *N. pumilio* runs between the steppe and the evergreen forests. The climate in this zone is cold-temperate with

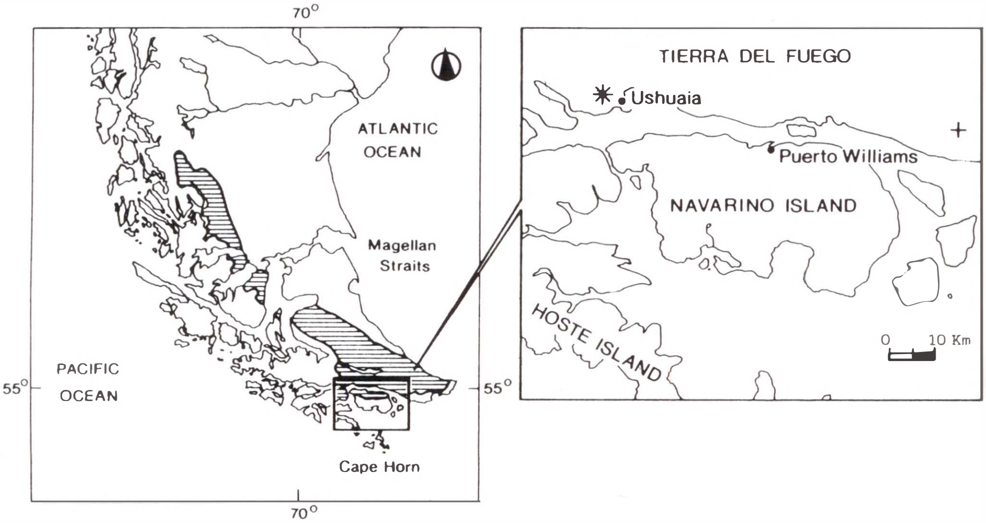

FIGURE 1. Location map. General distribution of *Nothofagus* forests on Tierra del Fuego. The striped area corresponds to the deciduous *N. pumilio* forest and the unstriped coast to the evergreen *N. betuloides* forest. The samples were taken in the Valle de Andorra (*) and the Costa de Moat (+).

steppe degeneration (Dfk'c; PISANO, 1981). Both types of forest are situated within the climatic limits of conifer forests (Fig. 3) (HAMMOND, 1972).

The flora and fauna of the different terrestrial ecosystems of Tierra del Fuego reflect the past and present effects of recent glaciations, climatic changes, and exogenous disturbances. This last factor is cited by PISANO (1975) as a lack of homeostasis.

On the forested mountain slopes numerous landslides bring about strong geomorphological and soil dynamism on different scales. Strong winds and shallow rooting cause many tree falls, creating gaps of different sizes and with the soil churned up and disturbed to varying degrees. Large quantities of wood debris are accumulated on the forest floor, in relation with the old-growth forest stands in some areas, and the unfavourable conditions for decomposition.

The severity of the climate marks an altitudinal gradient in the vegetation. The tree line rarely surpasses 700 m a.s.l. at these latitudes.

The morphology and degree of development of the trees are related to the altitudinal gradient. In the upper part of the forest and along a strip of more than 40 m above the timberline, trees take on a bushlike aspect, known as krummholz. At the tree line the height of the trees is less than 50 cm and *N. antarctica* usually appears as an accompanying species.

Studies on the forests of Tierra del Fuego have been mainly descriptive, especially biogeographic and taxonomic. Outstanding works are those of PISANO (1975, 1977, 1981) and DIMITRI (1982). Fluctuations in the extension of the forests based on pollen profiles as well as on other paleoecological features have been described by AUER (1960), MARKGRAF (1977) and VUILLEUMIER (1971). The climatic conditions, rainfall and temperature patterns have been analysed by ZAMORA & SANTANA (1979 a, b) and SANTANA (1984). Special reference should be paid to the work of SCHMIDT & URZÚA (1982) on the structure and production of *N. pumilio*, focused on forest management and timber production. The foliar anatomy of the species of *Nothofagus* has been studied by RAGONESE (1981) and the xylem anatomy by RIVERA (1987, 1988). We recently presented the first results on some aspects of soil-plant relationships for both types of forest (GUTIÉRREZ *et al.*, 1989).

There is, however, a lack of quantitive studies on most of the ecological aspects of these forests. The results of comparative studies carried out in the *N. pumilio* and *N. betuloides* forests are presented in this study. We have analysed the possible

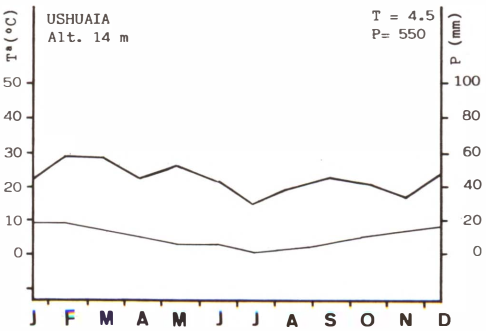

FIGURE 2. Climatic diagram according to the data from Ushuaia, Tierra del Fuego, 54° 48'S and 68° 19'W.

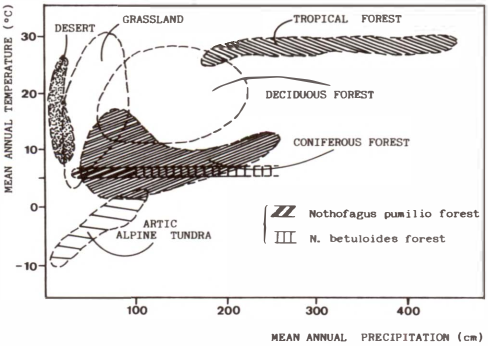

FIGURE 3. The ecoclimatic position of *Nothofagus* forests of Tierra del Fuego among the major terrestrial ecosystems in the ecoclimatic space defined by average temperature and precipitation (modified from HAMMOND, 1972).

causes of the distribution of the two species of *Nothofagus*, the former deciduous and the latter evergreen.

Climatic conditions are considered to be the primary cause of the distribution of these *Nothofagus* species, but other factors may also come into play. Soil characteristics may have a relevant role as well. On the other hand, apart from the research carried out by SCHMIDT & URZÚA (1982), no other studies have been undertaken concerning the structure and production of these forests and hence no data are available for the possibilities of exploitation and management techniques. The existence of great extensions of unexploited forest in Tierra del Fuego implies minimal human disturbance. Given the speed with which these ecosystems are being exploited for timber, crop and livestock all over South America, there is an urgent need for a database for a more rational management of the environment.

DESCRIPTION OF SAMPLING SITES

For the study of the two types of forest, two representative sites were selected on the Isla Grande de Tierra del Fuego (Republic of Argentina). The deciduous *N. pumilio* forest was sampled in the Valle de Andorra (54° 49'S & 68° 42'W) and the evergreen forest in the Costa de Moat (54° 49'S & 67° 21'W (Fig. 1).

The Valle de Andorra is 4 km north of Ushuaia. The annual average precipitation and temperature are 561 mm and 4.5 °C (HOLDGATE, 1960). The tree stratum is represented fundamentally by *N. pumilio*. The bottom of the valley is occupied by peat bogs of *Sphagnum* sp., with the forests developing on the mountain slopes, from 240 to 500-600 m a.s.l. In the lower and middle parts of the forest there are large emerging trees and discontinuities in the canopy. On the floor there is a large accumulation of wood, and young shoots appear in the clearings. Trees are smaller in the higher slopes of the mountains.

The evergreen forest was sampled in the area of Costa de Moat where the Beagle Channel exits towards the Atlantic, at around 110 km east of Ushuaia. Although climatic data are not available for this site, it is wetter and warmer than the Valle de Andorra. The area receives between 700 and 1000 mm of rainfall annually (ZAMORA & SANTANA, 1979a). An altitudinal gradient is also evident in this forest.

A mixed forest is formed in the lower parts, with *N. betuloides* forming the canopy. *Drimys winteri* Forst. and *Maytenus magellanica* (Lam.) Hook. f. form the understory, both species being broad-leaved and evergreen. This type of formation disappears at an approximate altitude of 150 m a.s.l., giving way to monospecific stands of *N. betuloides.* Isolated populations of *N. pumilio* also appear in well drained zones. The topography is gentler and the mountains are lower than in the Valle de Andorra. The upper forest limit reaches 350-400 m a.s.l., and is often limited by peat bogs which, in this zone, cover the higher parts of the mountains and extend over the middle parts, which are interconnected by gentle slopes.

METHODS

The recognition of different phases of forest development is based on the analysis of population structure of dominant species. Plots of 26 m x 26 m were delimited wherever possible in both types of forest in the upper, middle and lower slopes. Samples were gathered in each plot for the study of both trees and soils.

Estimation of biomass and production was carried out using dimensional analysis (WHITTAKER & WOODWELL, 1968; WHITTAKER & MARKS, 1975) from field measurements of trees. Diameter at breast height (DBH), at 1.30 m above

TABLE I. Climatic characteristics of 6 representative sites of the *Nothofagus* forest area. Due to their location they can be considered to encompass the gradient over which the forests extend. The data from Isla Nueva are the most representative of the zone in which the evergreen forest was sampled. Med: average annual temperature; Mmed: average of the maxima; mmed: average of the minima; Mabs: absolute maximum registered; mabs: absolute minimum registered. All the temperatures in °C. P, precipitation in mm yr^{-1}. Data from ZAMORA & SANTANA (1979a) except for those from Ushuaia.

SITE	LAT	LONG	Med	Mmed	mmed	Mabs	mabs	P (mm)
Punta Arenas	53°08'S	70°53'S	6.2	10.8	2.0	26.4	-11.8	438.9
San Isidro	53°47'S	70°59'W	5.9	9.0	3.1	22.0	-6.0	876.5
Ushuaia	54°48'S	68°19'W	5.4	9.6	1.2	29.5	-21.0	550.5
Puerto Navarino	54°57'S	68°20'W	6.4	8.9	3.3	23.2	-8.2	447.8
Puerto Williams	54°56'S	67°38'W	5.5	9.4	1.6	26.4	-10.0	553.4
Isla Nueva	55°10'S	66°36'W	5.6	9.3	2.8	23.8	-6.2	738.1

ground, tree height, and bark thickness were measured in all trees within the plots. Wood cores were extracted from the trunks at 1.30 m covering all the tree sizes in order to assess age structure, and to calculate increases in biomass and sapwood area. Production was estimated from the wood increments of the last ten annual rings. Branch and leaf biomass were calculated through allometric relationships from 6 trees of *N. pumilio* and 7 of *N. betuloides,* which were felled, measured and weighed.

All the trees in each plot were mapped in adjoining squares of 2 x 2 m, forming a lattice of 169 squares. Spatial structure was analysed with the hierarchical squares technique (GREIG-SMITH, 1964) and the distribution pattern was expressed as Morisita's index (WILLIAMSON, 1975; ELLIOT, 1983).

Total nitrogen and total carbon in leaves were measured with a Carlo Erba Autoanalyzer. Water-soluble phosphorus in the forest floor and mineral soil was determined using HUMPHREYS & PRITCHETT's (1972) procedure. A detailed explanation of the complete sampling methodology can be found in ROMAÑÀ *et al.* (1989).

THE DISTRIBUTION OF *NOTHOFAGUS* SPECIES

In a first approximation, the roles of continentality and of winter harshness in the dominance of deciduous over evergreen appear evident (Table I). This is also the explanation given from field observations. McQUEEN (1976), HUECK (1978) and PISANO (1977) attribute a strong resistance to low temperatures to *N. pumilio.* This explanation is supported by the presence of species with laurel-like leaves, such as *D. winteri* and *M. magellanica*, in the evergreen forest. These thermophile species are distributed along the coastline and at low altitude, in areas of relative climatic mildness where the evergreen forest is found. In the same way, evergreen flowering plants have a thermophile distribution compared with the deciduous flowering plants (WALTER, 1976), this character being interpreted as adaptation to extremely low temperatures.

The above explanation of the distribution of *Nothofagus* species is not entirely satisfactory. The existence of two distinct forest types is not related to a strong environmental gradient (Table I). Furthermore, both species are often found growing side by side. Yet, the transition from evergreen to deciduous forest takes place in just a few kilometers. The limits of each species could be both climatic and edaphic (PISANO, 1977). *N. betuloides* survives on soils with rather poor drainage, whereas *N. pumilio* is much less tolerant to waterlogging. The soils of the evergreen forest are predominantly hydromorphous, while the processes of podzolization are relevant in the deciduous forest (ROMAÑÀ *et al.*, 1989). The question thus arises as to

TABLE II. Specific leaf weight (mg cm^{-2}) for the two *Nothofagus* species. MO1, MO2 and MO3, sample sites from lowest to highest altitude in the *N. betuloides* forest on the Costa de Moat. VA1, VA2 and VA3, the same for *N. pumilio* in the Valle de Andorra. Date of sampling January 1989.

	species					
	N. betuloides			*N. pumilio*		
YEAR SITE	MO1	MO2	MO3	VA1	VA2	VA3
1 (1988)	14.35	10.89	12.55	8.28	8.61	9.14
2 (1987)	19.24	17.71	16.95			
3 (1986)	19.30	19.10	17.37			
4 (1985)	?16.10	19.33	18.15			
5 (1984)		18.54	18.59			
6 (1983)		18.91	19.20			
7 (1982)		20.04	19.61			

TABLE III. Percentage of carbon (C) and nitrogen (N) in leaves (one year leaves, * and two year leaves, +). MO1, MO2 and MO3, sample sites from lowest to highest altitude in the *N. betuloides* forest on the Costa de Moat. VA1, VA2 and VA3, the same for *N. pumilio* in the Valle de Andorra. LR, Lake Roca (near Ushuaia).

	% C	% N	C/N	Species
VA1	44.77	2.43	18.42	*N. pumilio*
VA2	45.22	2.10	21.53	*N. pumilio*
VA3	45.45	2.35	19.34	*N. pumilio*
MO1	49.50	1.67	29.64	*N. betuloides* (*)
	48.17	0.85	56.06	*D. winteri*
MO2	49.50	1.67	29.64	*N. betuloides* (*)
	49.58	1.18	42.02	*N. betuloides* (+)
MO3	49.80	1.32	37.73	*N. betuloides* (+)
LR	47.12	2.17	21.71	*N. antarctica*

the relative advantages of the deciduous or the evergreen habit.

The evergreen condition is advantageous for the absorption of nutrients when growth is limited by low soil nutrient concentrations. The evergreen character of *N. betuloides* gives it a certain independence from environmental fluctuations owing to a greater retention of nutrients in the tree. Furthermore, the longer lifespan of the leaves, up to seven years (Table II), allows greater photosynthetic production per nutrient unit in the leaves, increasing the efficiency of their use. This may represent an advantage both in habitats with low nutrient contents and those in which nutrient recycling is difficult. Sclerophyllous leaves of *N. betuloides* (RAGONESE, 1981) are adaptative in this kind of habitat. Average leaf density, an index of sclerophylly, is slightly higher than 8 mg cm^{-2} in *N. pumilio* and 17 mg cm^{-2} in *N. betuloides* (Table II). For comparison, *Fagus sylvatica* has values between 2.2 and 7 mg cm^{-2} in the Montseny mountains, NE Spain (TERRADAS, 1984), lower than those of the *Nothofagus* species. The index of sclerophylly calculated for *N. betuloides* (Table II) is similiar to that of the Mediterranean sclerophylles, whose values range between 10 and 25 mg cm^{-2} (SALA, 1986).

The differences in nutrient content between the two species are high. *N. pumilio* has large accumulations of nitrogen in its leaves (Table III). Thus, the C/N ratio reaches values around 20. In contrast, the nitrogen content in *N. betuloides* is low. Its C/N ratio is almost double, similar to the values found in *Quercus ilex*. In the soil, the C/N ratio is 40 in the Valle de Andorra, and 80 in the Costa de Moat, values much higher than those found in the leaves. The large accumulation of wood debris on the ground and the strong hydromorphism in the Costa de Moat, which retards the decomposition of organic matter, seem to cause these high concentrations of carbon on the ground.

In swamped boreal environments the sclerophyllous and evergreen habit of various species is associated with low nutrient contents in the plant tissues (LARSEN, 1982). This has been interpreted as an adaptation to restrictions imposed by a lack of O_2 in soil water, low temperatures in the radicular environment, absence of mycorrhizae, and the existence of free toxins. Mycorrhizae are indeed very abundant in the *N. pumilio* forest, and scarce under *N. betuloides*. The formation of mycorrhizae has been described for other *Nothofagus* species (MEYER, 1966). However, they have never been reported in waterlogged soils.

With respect to phosphorus, the differences between one type of soil and another are also pronounced (Table IV). The data for soluble phosphorus in the organic horizons of the deciduous forest are higher than average annual requirements of forest ecosystems in different environments (COLE & RAPP, 1981). Values for the evergreen forest range from average to moderately low. Sclerophylly is present in some Australian species in spite of high rainfall; the anomalous presence of this trait has been attributed to low soil fertility, because the sclerophylly index decreases after the addition of nitrogen and phosphorus (BEADLE, 1966). Likewise, in well aerated soils at mid-latitudes, sclerophylly has been related to low availabilty of nutrients, especially phosphorus (LOVELESS, 1961).

The decomposition of organic matter and the release of nutrients in waterlogged soils is slower than that expected under cold climates with low temperatures and minimum thermal fluctuation. Waterlogging of the soil appears to be related to the distribution of the two species in the Valle de Andorra and in the Costa de Moat. The characteristics of hydromorphic soil would promote physiological strategies for nutrient conservation in the trees, together with a greater efficiency in nutrient use. The maintenance of the leaves throughout the year, as well as their greater longevity and strong retranslocation of nutrients, can be interpreted as adaptative in this context. Such a strategy is possible under climatic conditions allowing the persistence of leaves in winter. Slight differences in the absolute minimum temperatures seem to be sufficient for the establishment of such conditions, as shown by the climatic data in Table I.

At the regional level, however, the hypothesis of hydromorphy is still questionable, as it is difficult to imagine that a parameter of this type could have such a pronounced geographical component. One element to consider is that the distribution area of *N. betuloides* roughly coincides with the rainier coastal areas. In addition, these southernmost areas seem to have been more affected by glaciation, producing gentle slopes which facilitate water accumulation.

TABLE IV. Water soluble phosphorus (Kg P ha^{-1}) in the organic layer, H, and in the first 15 cm of mineral soil. MO1, MO2 and MO3, sample sites from lowest to highest altitude in the *N. betuloides* forest on the Costa de Moat. VA1, VA2 and VA3, the same for *N. pumilio* in the Valle de Andorra.

	Available P (kg P ha^{-1})			
	H		0-15	
SITE	MEAN	STD	MEAN	STD
VA1	14.33	6.79	0.5	0.08
VA2	22.03	3.42	0.2	0.08
VA3	11.68	4.36	0.4	0.22
MO1	2.30	1.27	0.4	0.22
MO2	4.13	3.02	0.1	0.01
MO3	12.10	2.55		

STAND STRUCTURE

The distribution of size frequencies, either of DBH or of the biomass of individuals, is frequently used to characterize the structure of a forest stand, together with the ranges and values of the other variables. Although without common agreement regarding the size interval used by different authors, we have defined twelve size classes of DBH (FORD, 1975; MOHLER *et al.*, 1978; Figs. 4 and 5). These distributions reflect the differences of the forest stands according to altitude. The biggest trees grow in the lower and medium slopes, where better edaphic conditions and a milder climate prevail. Other parameters reflect these differences among stands. Yet the density of trees is quite high in the upper slopes. Thus, the basal area increases with elevation as a consequence of the greater packing together of individuals.

Dendrochronological values at 1.30 m tend to underestimate tree age. Hardwood of some cores was rotten so the age was estimated dividing the tree radius by the annual mean increment. To avoid over- or underestimation of tree ages, cores rotten to more than half of tree radius were rejected. In this manner, our results indicate that the biggest trees are not always the oldest (Fig. 6). Tree ages show a high variation with respect to size in both forests. This may be a consequence of the great heterogeneity of habitats. In the evergreen forest, a high variability is also found in the ages reached within a narrow category of DBH, especially above 45 cm. In contrast with *N. pumilio*, *N. betuloides* reaches older ages with smaller diameters. This may be related to the oligotrophic condition of the soil in which the latter species grows (Table IV). Nevertheless, differences exist among the stands according to the site characteristics. In the lower slopes of the evergreen forest, classes of DBH less than 25 cm do not exist and there is no clear relation between age and DBH. In the remaining stands the relationship between size and age is more evident and could be statistically described by allometric and/or exponential functions.

The structure of a forest is dynamic. It changes over time and depends on the ecological characteristics of both the component species and the whole habitat. The dependence on the characteristics of the species is manifest in the degree of tolerance to shade. This trait determines to a large extent the way in which regeneration is produced and is reflected in size and age structure of the stand. The more shade-tolerant species tend to form multiple-cohort stands and tree recruitment is continuous throughout time. On the other hand, when the trees vary little in size and have originated in a relatively short interval of time, the structure of the stand is even-aged, corresponding to single-cohort stands. This type of stand can be formed by shade-tolerant or shade-intolerant species, although even-aged stands of intolerant species are more common. According to the literature, *Nothofagus* species are shade-intolerant (HUECK, 1978). Thus, the expected distribution of DBH's would correspond to that of even-aged stand forests (cf. SCHMIDT & URZÚA, 1982). Most of the observed size distributions are bimodal (Figs. 4 and 5). The regenerating class, formed by trees with less than 7 cm of DBH, is scarce or lacking in many stands except the one in the lower part of the Valle de Andorra (Fig. 4) and in the upper slope of Moat (Fig. 5). But hardly any of these stands can be considered uneven-aged. The bimodal distributions correspond more to the final stage of

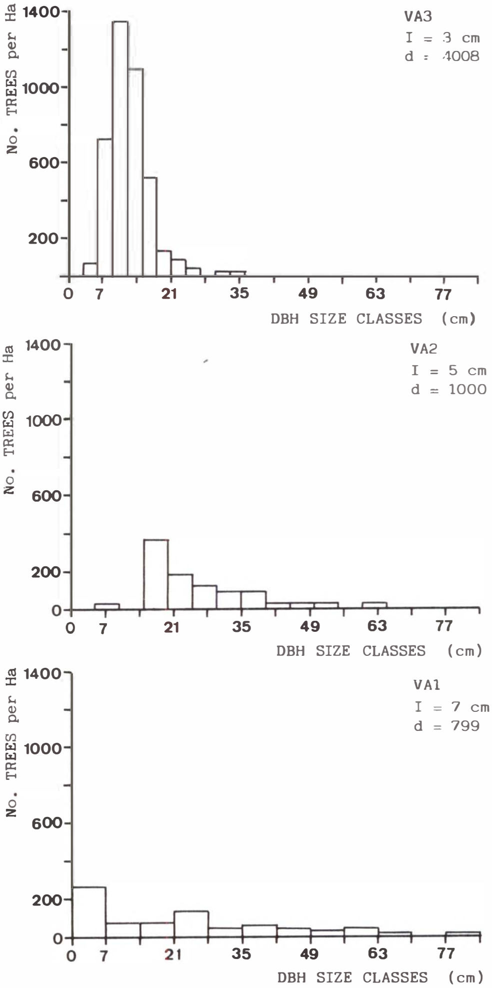

FIGURE 4. Distribution of trees according to the DBH sizes in the lower (VA1), medium (VA2) and upper (VA3) slopes of the deciduous *N. pumilio* forest in the Valle de Andorra. Notice that the interval (I) defining size classes and the density of the stand (d, number of trees per hectare) varies among sample plots.

self-thinning and even-aged stands of mature forest. In these stages of development, distributions are often indeed bimodal when twelve size categories are used (FORD, 1975; MOHLER *et al.*, 1978). Bimodality is a consequence of the aging of the stand in which the largest size categories in trunk diameter and tree height form a distinct group of trees. When age is considered (Fig. 6), most of the stands cannot be classified as even-aged, except the plot of the higher slope in the Valle de Andorra.

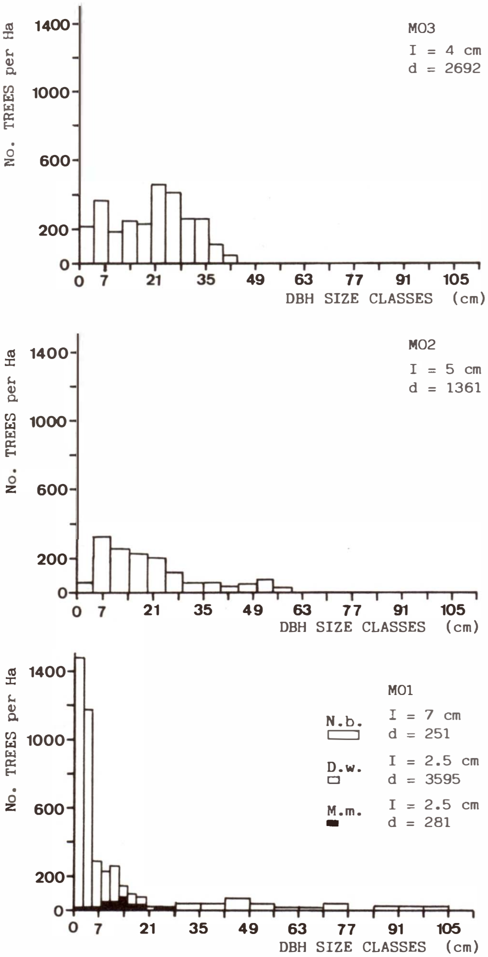

FIGURE 5. Distribution of trees according to the DBH sizes in the lower (MO1), medium (MO2) and upper (MO3) slopes of the evergreen *N. betuloides* forest on the Costa de Moat. Notice that the interval (I) defining size classes and the density of the stand (d, number of trees per hectare) varies among sample plots. Data are also given for *Drimys winteri* (D.w.) and *Maytenus magellanica* (M.m.).

Analysis of the spatial distribution of all the trees in the plots gives clues to the regeneration pattern. Two examples of spatial distribution are shown in figure 7 for the lower part of the Valle de Andorra, VA1, and the higher part of the Costa de Moat, MO3. In the first case, regeneration is produced in areas free of large individuals. Therefore, the bimodality observed in DBH size distributions (Figs. 4 and 5) may be due to the recruitment in bursts of new individuals when the canopy has disappeared. Although it is not known up to what point the *Nothofagus* species are shade-intolerant, it is very significant that in the low part of the Costa de Moat where the *N. betuloides* forest has *D. winteri* and *M. magellanica* in the understory, there are

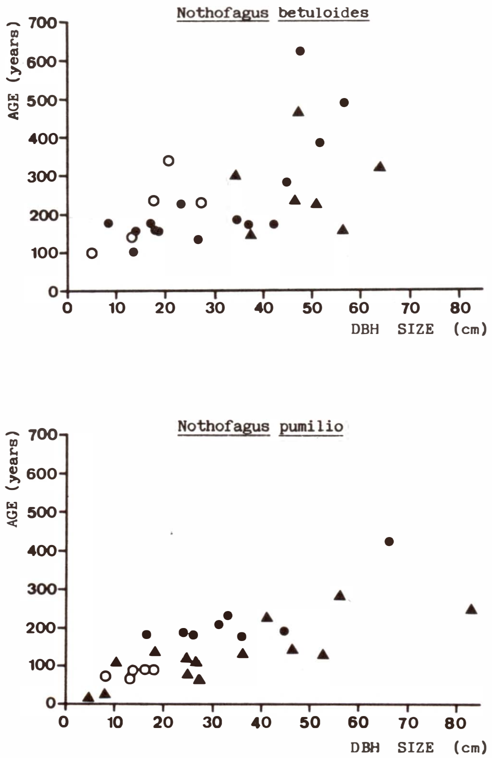

FIGURE 6. Relation between age and size of trees in 6 sampled plots. Data from the lower (triangles), middle (filled circles) and upper (open circles) slopes of each type of forest.

neither saplings nor poles (Fig. 5, MO1).

If the recruitment of new individuals is produced in bursts and these *Nothofagus* species do not regenerate beneath their canopy, the regenerating class should exhibit a spatial pattern in accordance with environmental minor disturbances. Spatial analysis was carried out twice, once for the large trees, with a DBH above 30 cm, and then including all the trees. The results are displayed in figure 8. The large trees feature a regular distribution in small areas (Morisita index values of less than one), which becomes random as the area increases (Morisita index values around one). However, when all the trees are included, the distribution is aggregate up to areas of 64 and 80 m^2 in the low and medium parts of both forests, and 16 and 36 m^2 in the higher parts. These cluster dimensions indicate that the recruitment of new individuals is produced in a discontinuous form and in a space defined by other physical attributes. The result is a mosaic of patches of sizes and ages, sometimes overlapping and sometimes distinct (cf. PEET & CHRISTENSEN, 1987). The development of these patches may be subpopulations or different groups of trees, but other new ones also appear as the distributions of diameters (Figs 4 and 5) and ages (Fig. 6) seem to indicate. On the other hand, the spatial distribution of trees is very different between the upper and lower slopes of both forests (Fig. 7). The distribution of large trees in the upper parts is aggregate, the clusters being of 16 and 32 m^2. When all the trees are included the size of the patches is 4 and 8 m^2, these being included in the former clusters. The smaller clusters present in the higher parts of the forest correspond to a different type of regeneration, i.e. vegetative. Regeneration is accomplished by sprouting at the base of the trunks of living trees. This type of regeneration renders a different pattern from those of the lower and middle parts of the forest.

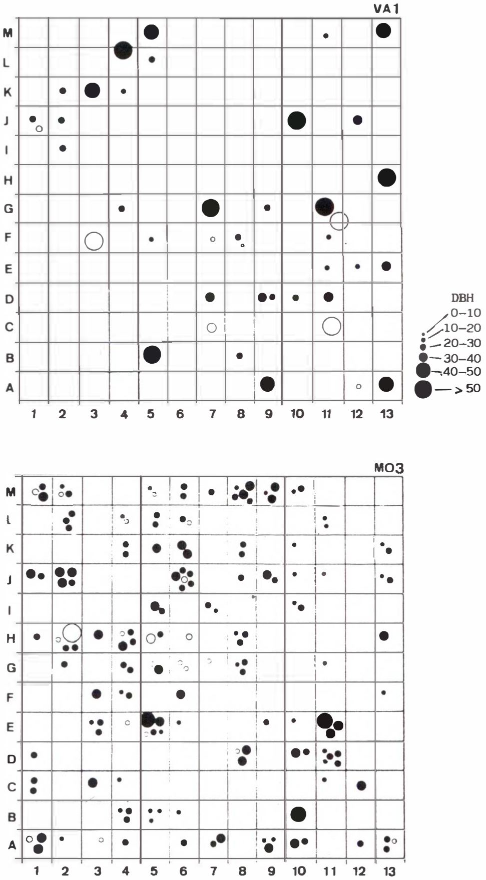

FIGURE 7. Spatial distribution of the trees in the lower slope of the Valle de Andorra (VA1) and in the upper slope of the Costa de Moat (MO3). The distribution at middle elevations is very similar to that of the lower slopes. DBH in cm, grid in m. White circles represent dead individuals.

Another very important structural parameter is the leaf area index, LAI. The leaf area index is fairly similar in all the sampled plots; values are between 2.3 and 4.5 m^2 m^{-2}, being higher in the evergreen forest (Fig. 9 and Table V). The range of values for the leaf area index are coherent with those expected according to latitude, climate, and the structure and dynamics of forest stands subjected to frequent treefalls. *Fagus sylvatica* features values of 3.2 in leaf area index at similar latitudes in the Northern Hemisphere owing to the harsher climate (De ANGELIS *et al.*, 1981).

The relation between leaf area and sapwood area is interesting due to their mutual functional implication. These *Nothofagus* species are diffuse-porous with only small-diameter vessels (RIVERA, 1987, 1988). In principle, this implies a smaller LAI per unit of sapwood with respect to ring-porous trees such as oaks. The values found for *N. pumilio* are 0.12 and 0.13 m^2 cm^{-2} in the stands situated in the medium and lower slopes and 0.07 m^2 cm^{-2} in the upper slopes. Results show that a greater sapwood surface is needed in the stand of the subalpine zone, i.e. the area of evaporation per unit of sapwood area is lower. These variations may reflect aspects related to the permeability of the wood, the increased viscosity of water, a possible adaptation to more dessicant conditions imposed by wind and a higher demand of carbohydrates. The values are similar to those found for *N. solandri* in montane and subalpine stands, respectively (BENECKE & NORDMAYER, 1982, in WARING & SCHLESINGER, 1985). The ratio of leaf to sapwood area calculated for the stands of *N. betuloides* forest, gives values of 0.32 m^2 cm^{-2} for the lower slope close to the sea and 0.11 and 0.09 m^2 cm^{-2} for the medium and upper slopes, respectively. The requirements of the sapwood area appear to be reduced in the milder climate, particularly in the lower coastal location. These and other previously mentioned differences among stands at different elevations may be due to either genetic differentiation (WARING & SCHLESINGER, 1985) or environmentally dependent different gene expressions.

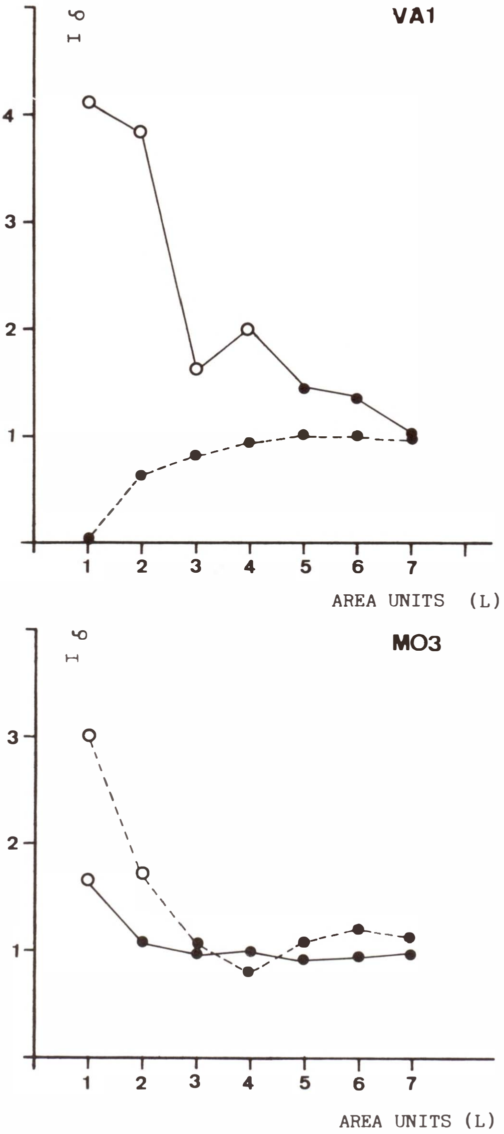

FIGURE 8. Representation of the values of the Morisita index (Id) according to area. Each area unit measures $(2 * L)^2$ m^2, L being the unit of length. Open dots are data points significant to 95 % according to the F test. The values around 1 are those that take a random distribution, those over 1 appear in aggregates, and those below 1 are regular. The broken line corresponds to trees with DBH > 30 cm, the continuous line to all trees in the plot.

BIOMASS, PRODUCTION AND SOIL ORGANIC MATTER

The range of aboveground biomass and production values is shown in Table V. The evergreen forest features a greater biomass but a lower production than the deciduous forest. This difference translates into a lower biomass turnover rate for the former. The *Nothofagus* forests of Tierra del Fuego have climatic conditions corresponding to the zone of boreal conifer forests (Fig. 3), but show higher biomass values than the latter (Table V). This is not observed in the *N. pumilio* stands of the upper slope, with a production of 148.0 g C m^{-2} yr^{-1}, a figure that lies in the low range of observed values. High values of biomass are translated into a much lower productivity and a higher turnover rate in relation to the boreal forests. These data agree with the results and conclusions that refer to other structural parameters.

TABLE V. Structural characteristics, including biomass and production, of the *Nothofagus* forests sampled in Tierra del Fuego.

	Deciduous forest	Evergreen forest
Age	91 - 247	339 - 628
Trees ha^{-1}	799 - 4008	251 - 2692
LAI (m^2 m^{-2})	2.3 - 2.8	2.5 - 4.5
Basal area (m^2 ha^{-1})	50.5 - 66.9	62.6 - 107.7
Biomass (kg C m^{-2})	6.0 - 13.6	10.5 - 15.6
Production (g C m^{-2} y^{-1})	148.0 - 372.1	204.6 - 346.4
Leaves (g C m^{-2} y^{-1})	85.3 - 100.6	90.2 - 143.5
P/B (yr-1)	0.022 - 0.031	0.018 - 0.027
B/P (yr)	46 - 32	56 - 37
	Boreal Forests	Temperate Forests
Biomass (kg C m^{-2})	2.5 - 16.6	2.5 - 25.7
Production (g C m^{-2} yr^{-1})	166.7 - 833.4	250.0 - 1041.8

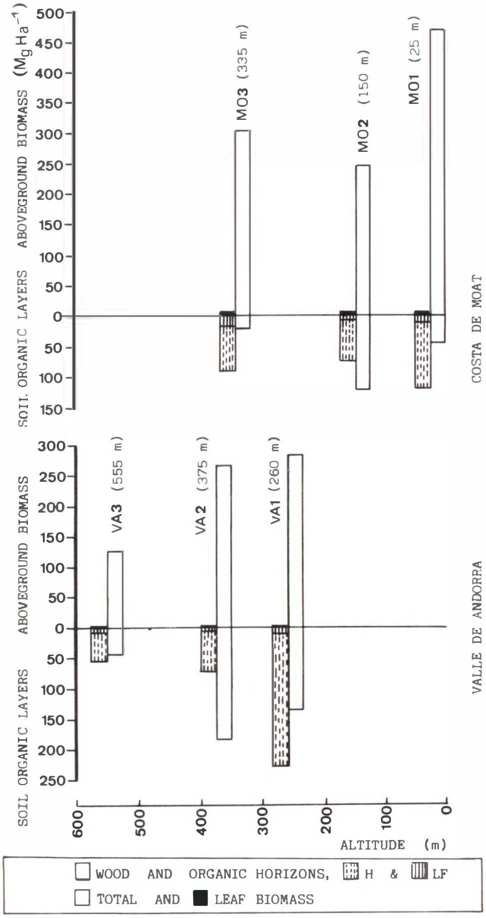

FIGURE 9. Distribution of biomass and soil organic matter, both in Mg ha^{-1}, in the 6 sampled plots.

Relative to the incident radiation, the evergreen forest has a greater average production efficiency than the deciduous one. Values range from 0.32 to 0.54%, and from 0.17 to 0.44%, respectively. In the relevant calculations involved we considered the average incident radiation in each area (ZAMORA & SANTANA, 1979a). The average estimated incident radiation for the deciduous forest is 85 Kcal cm^{-2} yr^{-1}, and that of the evergreen forest is 65 Kcal cm^{-2} yr^{-1}. Although these data are not referred to the sampling stations, they provide an adequate quantification. The efficiency of these forests appears to be low, being more similar to that of hardwood than coniferous forests (WEBB *et al.*, 1983), in spite of having climatic similarities with the latter. But if we consider relations such as the production of wood relative to leaf biomass (Fig. 10), the *N. betuloides* forest has a lower wood production per unit of photosynthetic surface than *N. pumilio*. Furthermore, given that *N. betuloides* has a greater LAI its growth efficiency, expressed in g of wood per m^2 of leaves per year, is lower, being situated in an intermediate position between the hardwood and the coniferous forests. On the other hand, *N. pumilio* overlaps with hardwood forests (Fig. 10, O'NEILL & De ANGELIS, 1981). In general, the restrictions on accumulating and maintaining high leaf area indices are greater in cold climates. Besides the effect of climate, in Tierra del Fuego the following factors should be considered: windfall disturbance, fungal disease, landslides and snow-related dynamism of soil, all of which prevent higher LAI and leaf biomass values. If indeed, forests that do not reach and maintain an LAI of 6 do not reach a steady state (WARING & SCHLESINGER, 1985), the forests of Tierra del Fuego may be an example of forests that do not reach a successional steady state.

In the general context of production in terrestrial ecosystems, the accumulation of biomass in the forests of Tierra del Fuego appears to be limited by low temperatures. Temperature is indeed one of the main factors limiting production although it is not adequately described by means of simple statistical relations (WARING & SCHLESINGER, 1985). This dependence on temperature is also conspicuous at a local level along the altitudinal gradient in the Valle de Andorra. The limitations on potential production in the upper slope of the deciduous forest can be related to a harsher climate. On the other hand, soil conditions may have a greater importance in the evergreen forest (Table IV, Fig. 9). Thus, the altitudinal gradient is blurred by the heterogeneity of soil hydromorphism.

In agreement with the structural and dynamic characteristics, the amount of organic material accumulated in the forest soil of Tierra del Fuego is high (Fig. 9). The climatic conditions, low temperatures and an average annual fluctuation that does not exceed 8 °C, favor a slow decomposition. The accumulation of organic matter on the soil results from the balance between litter inputs and the rate of decomposition, the former being dependent upon forest production. The rate of decomposition is determined by the climatic conditions, the nature of the litter, and the characteristics of the soil itself. The soil characteristics, e.g., waterlogging and chemical conditions, affect, in turn, biological activity. Thus, the rate of decomposition integrates the biological potential of the soil and determines both the turnover and availability of nutrients for plants, mainly N and P. The decomposition rate can be considered as a soil fertility index.

In the topographic sequence of the Valle de Andorra, the organic matter, and especially the wood debris in the organic horizons, decreases from the lower to the upper slopes, in accordance with biomass (Fig. 9). These results indicate that the differences in organic matter content are explained by the quantity of litter fall. Furthermore, the harsher climate in the upper slopes does not appear to delay the decomposition of organic matter. Since the estimated contribution from leaves is

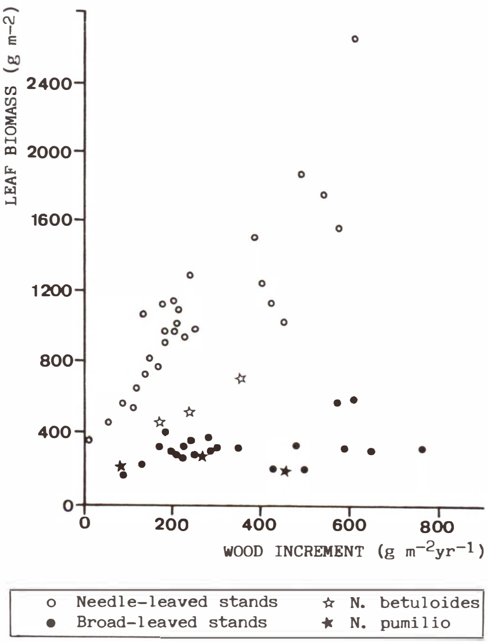

FIGURE 10. Wood production in relation to leaf biomass of the sampled *Nothofagus* forests in Tierra del Fuego, together with published data for other forests (O'NEILL & De ANGELIS, 1981). Notice the similarity of the evergreen *N. betuloides* with coniferous forests and of deciduous *N. pumilio* with hardwood forests.

similar in the three plots (Fig. 8, Table IV), the differences in litter accumulation must be accounted for by the wood fraction.

The accumulation of organic matter in the sampled stands of the evergreen forest, in contrast to the Valle de Andorra, increases from the lower to the upper parts. This difference is conditioned by the role of excess of water in the evergreen forest, where it causes a great spatial variability in the accumulation of organic matter. Decomposition takes place temporarily under anaerobic conditions, which are quite restrictive to mineralization. The H soil horizon in the stands on the lower slopes of both forests has a high mineral content, probably due to more intense biological activity. A lot of worms were observed during sampling.

High amounts of litter and wood debris may control the long-term productivity of forest communities (CHARLEY & RICHARDS, 1974). The accumulation of organic matter in the H horizon is very high in the forests studied: up to around 200 Mg ha^{-1} in Valle de Andorra and 135 Mg ha^{-1} in Costa de Moat (Fig. 9). These values are similar to those found in the boreal coniferous forests of Vancouver, 50^{o} N of latitude (VALLEJO, 1987). In contrast, typical Mediterranean forests, such as those of evergreen *Quercus ilex* in Montseny, NE Spain, reach only 10 to 50 Mg ha^{-1} (HERETER, 1990).

The H horizon has plenty of tree roots in both *Nothofagus* forests. However, in Moat most of the roots usually do not reach the mineral horizons because of waterlogging. Also, the H horizon has the highest concentrations of nutrients in the soil (Table IV). Therefore, the H horizon plays a key role in the maintenance of soil fertility. Rational forest management practices should take this into account.

The rate of decomposition (k; OLSON, 1963), calculated for the LF horizon and taking into account the estimated contribution of fallen leaves from Table V, ranges between 0.20 and 0.38 in the stands sampled. These values indicate a relatively rapid incorporation of litter remains into the H horizon. The mean residence time of leaves in the LF horizon, that is 1/k, ranges between three and five years. However, the values of k, calculated for the leaf fraction, may be underestimates, since wood debris less than 2 cm in diameter were included. These woody remains were not included in the estimates of litter fall. The mean residence time for all litter fall including leaves and coarse wood debris ranges from 15 to 60 years in both *Nothofagus* forests.

CONCLUSIONS

The forest landscape of Tierra del Fuego has a mosaic pattern at different spatial scales. Within a given forest type, patches of younger trees are included in the biggest patches of old forest. This structure may be caused by strong disturbances like landslides and windthrown trees in the slopes. The gaps produced after such events are colonized by *Nothofagus* seedlings, while there is little tree regeneration under the old-growth forest canopy. The result is multicohort stands. There is also a clear altitudinal gradient in forest structure, the extreme conditions of the upper slopes preventing the development of old-growth forests.

Owing to the limititations imposed by climate, the *Nothofagus* forests of Tierra del Fuego have low productivity. These unexploited forests have a temperature-limited accumulation of biomass and production. Yet there is a huge accumulation of organic matter on the forest floor with an important contribution of decaying wood. The large amounts of accumulated litter reflect the slowness of the decomposition process and the stage of the forest.

In adverse soil conditions, such as waterlogging, the evergreen *N. betuloides* is the dominant forest species. However, it has a lower productivity than *N. pumilio*, even though it is distributed in the rainier and milder areas of Tierra del Fuego.

Broad-leaved evergreen trees are exceptional in extreme latitudes whereas they are common in very different habitats, such as under Mediterranean type conditions. This study shows that the evergreen and sclerophyllous characteristics of *N. betuloides* are related to shortage of nutrients in waterlogged soils. This is a physiological limitation similar to those attributed to typical Mediterranean ecosystems in much drier conditions.

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