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Laurophyllisation of deciduous *Nothofagus*-Forests in Southern Chile

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Abstract

Stratified measurements of frequency of the major tree and liana species have been used to interpret the vegetation dynamics of deciduous *Nothofagus obliqua* forests in the Central Valley of south-central Chile. In terms of both cover and frequency, secondary forests are dominated by *Nothofagus obliqua* in association with evergreen and laurophyllous-indifferent species. Laurophyllous trees of Valdivian origin, such as *Aextoxicon punctatum,* dominate all strata of the few remaining old growth forests, most of them showing regeneration patterns typical of shade tolerant late-sucessional species. Evergreen tree species from Central Chile which reach their southern limit in the study area are most frequent in early successional stages on "zonal" sites, although their original niches in this region were “extrazonal” thermophilous sites. The current dominance of the deciduous *Nothofagus obliqua* appears to be a consequence of anthropogenic destruction of stands during the last century. Long periods without disturbance would cause these forests revert to evergreen broad-leaved rain forests. This laurophyllisation process appears to be controlled by land-use practice and intensity rather than by global warming. Consequently, studies on laurophyllisation should pay particular attention to land-use history and changing patterns of land-use.

Introduction

The Central Valley of the IX. Region of Chile is a transition zone between the evergreen-sclerophyllous forests of mediterranean Central Chile and the Valdivian rainforests of perhumid Southern Chile. During the last 150 years the previous, more or less continuous, forest ecosystems of this ecotonal zone have been destroyed by extensive burning and logging, and primary forests have almost disappeared outside the national parks. The extant secondary forests in this ecotonal zone of Southern Chile are dominated by deciduous *Nothofagus obliqua* with regenerating laurophyllous species in their understories. This fact has provoked a long-lasting debate about how these forests should be classified. Most classifications and vegetation maps classify the forests of this transition zone as deciduous (Schmithuesen 1956, Hueck 1966, Gajardo 1994),but the composition of their understories seems to support the hypothesis that laurophyllous species are invading these, apparently deciduous, forests. Contemporary phytosociology allows both the classification of vegetation units and analysis of kinetics of vegetation dynamics. The objective of this study is to investigate the vegetation dynamics of these *Nothofagus obliqua* forests by analyzing their species composition and structure. Veblen et al. (1979) studied *Nothofagus obliqua* forests in the Andean precordillera and emphasised the natural disturbance regime of this region with its high frequency of catastrophic events caused by volcanic eruptions, fires or earthquakes. Near Temuco, however, similar *Nothofagus obliqua* forests are found on old and stable Tertiary land surfaces, far from the volcanic disturbances of the Andes. Our hypothesis is that the dominance of *Nothofagus obliqua* is man-made and due to land-use and that, without anthropogenic disturbance, laurophyllisation will lead to evergreen broad-leaved forests.

Study area

The study area is situated directly north-west of Temuco, the capital of the IX. Region of Chile, at about 38°40' S and 72°40' W. It occupies an area of ca. 500 km^2 and is characterized by a mountain chain formed by continental-volcanic materials which ascends to 770m a.s.l. and a lower part with gently rolling hills formed from marine sediments. The lower parts (below ca. 300m) are covered by old red clay soils (Ultisols), and are separated by a heterogeneous transition zone from the upper parts (above ca. 500m) which have young volcanic ash soils (Andosols).

The climate of the study area is intermediate between perhumid Southern Chile and the mediterranean climate of the Central Zone. Temuco has an annual rainfall of about 1300mm with a mean temperature of 11.6°C (Walter 1990). Most of the precipitation falls during the mild winter and there is typically an arid period of about two months in summer (van Husen 1967). The concurrence of relatively cool air temperatures (due to the proximity of the Humboldt Current) and high insolation (due to the subtropical latitude) favours high photosynthetic rates and low respiratory losses that result in highly productive forests (Schwabe 1956).

At lower altitudes, the study area is dominated by deciduous *Nothofagus obliqua* forests corresponding to the Nothofago-Perseetum lingue (Schmithüsen 1956, Oberdorfer 1960). Above ca. 500m, the forest remnants are classified as Nothofago-Dasyphylletum (Finckh 1995) and contain species such as *Nothofagus alpina*, *Dasyphyllum diacanthoides* and *Myrceugenia planipes*. Neither these "highland forests" growing on young volcanic ash soils nor the myrtle forests growing on hydromorphic soils along the rivers are considered further in this paper.
The remaining forest patches are surrounded by combinations of three types of land-use: extensive subsistence agriculture of the Mapuche Indians, intensive agriculture associated with large farms, and forest monocultures of introduced *Pinus* and *Eucalyptus* species. Most of the remaining native forests are secondary, but two remnants of more or less primary forest vegetation still exist in the mountainous part of the study area, about 10km north of Temuco. The "Reserva Nacional Cerro Ñielol" (80ha, ca. 100 - 300m) and "Rucamanque" forest reserve (450ha, ca. 200 - 550m). Each of the two forest remnants represents a different type of the formerly widespread forests of the area. The Reserva Nacional Cerro Ñielol (henceforth called "Ñielol") represents a forest type which has, to some extent, warmer and drier "extrazonal" site conditions, whereas the site at "Rucamanque" provides the cooler and more humid conditions characteristic of the "zonal" type of these forests. "Rucamanque" has lower human impact than "Ñielol", with 45% of its area typical of primary forest.

Methods

Black and white aerial photographs (FONDEF 1994, 1:20.000) were used to map the actual forest vegetation of the study area. Information about land-use history was obtained from aerial photographs dating from 1945, 1961 and 1988 and from bibliographic sources (e.g. Berninger 1929). The results were digitized and processed with a Geographic Information System (ATLAS-GIS).
Subsequently, we checked the composition of the forest vegetation of 93 stands, using modified Braun-Blanquet (1964) methodology. The vertical structure of the stands was recorded in seven different strata with three tree layers (T1 > 20m, T2 20m - 10m, T3 10m - 5m), a shrub layer (S 5m - 0.5m), a field layer (F < 0.5m) and two layers for epiphytes and lianas (L1 lianas in T1 - T3, L2 lianas in S and F). These structural divisions allow the regeneration dynamics of the different species to be analyzed. The cover of each species in the 7 different vertical layers was estimated by the Braun-Blanquet-Scale (5 = 75 % - 100 %; 4 = 50 % - 75 %; 3 = 25 % - 50 %; 2 = 5 % - 25 %; 1 = 1 % - 5 %; + < 1 %). The frequency of each species in each layer was calculated as a percentage of the number of stands. We defined five stand-types for statistical analysis: young/low secondary forests not reaching the T1-layer, older/taller secondary forests with canopy reaching the T1-layer, (more or less) intact old

growth forests and extrazonal stands of secondary and primary forest containing *Cryptocarya alba* (a mediterranean element indicating warmer and drier site conditions). Due to small numbers of stands, secondary forests containing *Cryptocarya alba* were not separated into low and tall secondary forest.

Statistical analyses were confined to liana and tree species capable of reaching heights of more than 10m that also reached at least 15 % frequency in one of the layers of at least one stand type. The relative importance of the trees was estimated by averaging the median values of each Braun-Blanquet score in each stand-group.

Climatic measurements were obtained from three stations in open areas.

Results

Species composition and structure

Figure 1 maps the distribution of forest vegetation in the study area, and includes both native forests and plantations of introduced species. The former continuous forest of the study area is now highly fragmented with less than 1 % of the total area still covered by old growth forest; ca. 6 % with deciduous *Nothofagus obliqua* forest and 9 % covered by degraded shrublands.

The selected tree species and lianas have been classified according to ecological types and life forms (Figure 2). Figure 3 shows the mean frequency of the selected tree species in the various layers and forest types. In secondary forests, deciduous *Nothofagus obliqua* has the highest frequency of any tree. He occurs with high frequency in all vertical strata of secondary forests less than 20m high, including those with *Cryptocarya alba* (the extrazonal type). In these latter forests, *Nothofagus obliqua* has its highest frequency values in the T3 layer, indicating successful regeneration of this deciduous tree. The taller secondary forests show a similar pattern, with the peak frequency of *Nothofagus obliqua* in the T1-layer and decreased frequencies in the lower strata. In the two primary forest-types, *Nothofagus obliqua* shows a different pattern, and appears mostly as an emergent in the top layer (T1) but is almost absent from all other strata, indicating an almost complete inhibition of *Nothofagus obliqua* regeneration in both primary forest types.

The pattern of frequencies of the other tree species in the different forest types show marked differences to that of *Nothofagus obliqua*. The high frequencies of "evergreen-mediterranean" trees in the understory of the extrazonal secondary forests and less tall secondary forests indicate successful regeneration under the canopy of *Nothofagus obliqua*. *Peumus boldus* and *Cryptocarya alba* reach the main canopy of the primary forests of the warmer and drier sites but are almost absent from the zonal primary forests. *Citronella mucronata* and *Maytenus boaria* seem to be restricted to disturbed secondary forests in the study area, and *Podocarpus saligna* shows a similar pattern.

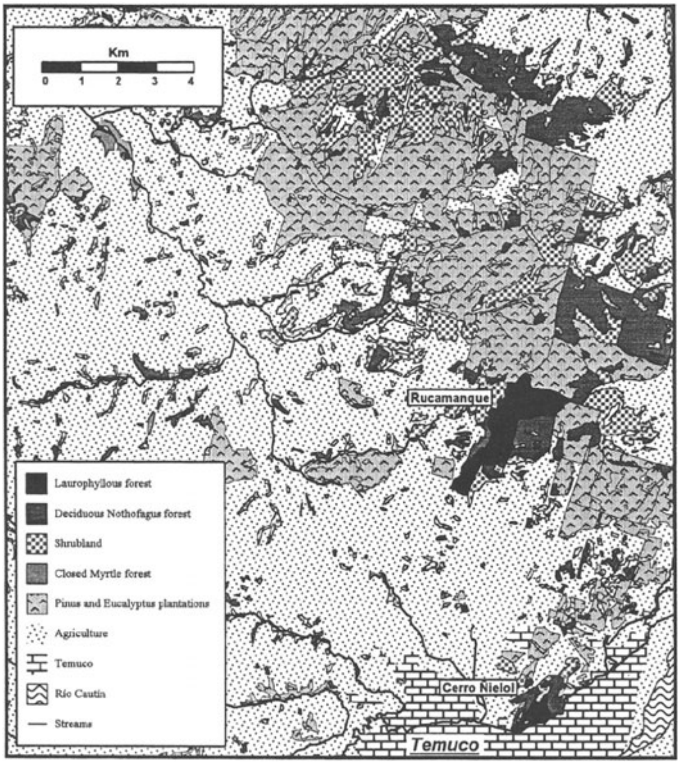

Figure 1: Vegetation map of the study area

Deciduous tree species:	**Evergreen tree species:**	**Laurophyllous-indifferent tree species:**	**Laurophyllous-Valdivian tree species:**
Nothofagus obliqua	*Cryptocarya alba* *Peumus boldus* *Citronella mucronata* *Maytenus boaria* *(Podocarpus saligna)*	*Persea lingue* *Laurelia sempervirens*	*Aextoxicon punctatum* *Eucryphia cordifolia* *Laureliopsis philippiana* *Lomatia dentata* *Gevuina avellana* *Weinmannia trichosperma*
Deciduous lianas:	**Geophytic lianas:**	**Laurophyllous-indifferent lianas:**	**Laurophyllous-Valdivian lianas:**
Muehlenbeckia hastulata *Rubus constrictus*	*Bomarea salsilla* *Dioscorea auriculata*	*Boquila trifoliolata* *Cissus striata* *Lapageria rosea* *Lardizabala biternata*	*Elytropus chilense* *Hydrangea serratifolia* *Luzuriaga radicans* *Mitraria coccinea* *Pseudopanax valdivianum*

Figure 2: Species classification according to ecological types and life forms

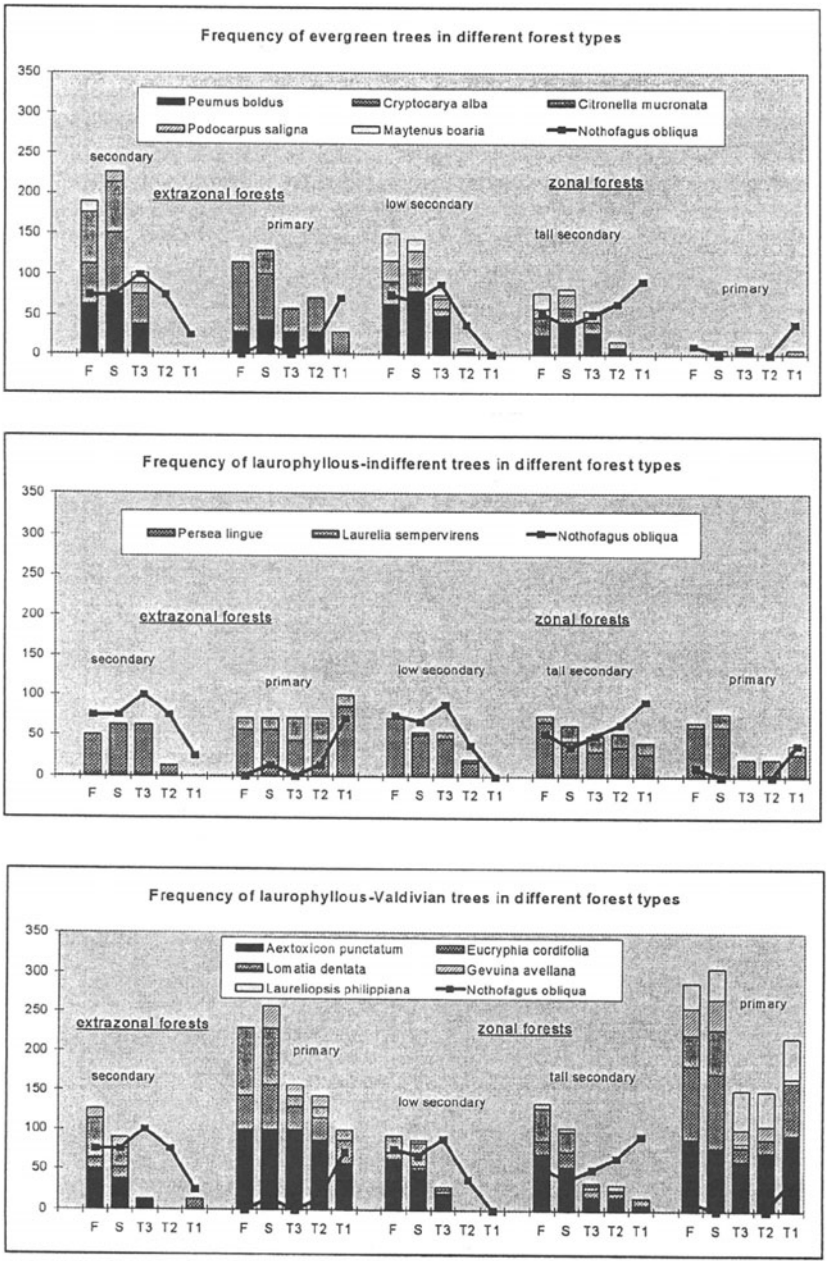

Figure 3: Mean frequency of selected tree species in different forest types

The laurophyllous-Valdivian tree species are rarely present in the canopy of the secondary forests, but their high frequency in the understory of these stands indicates that they are regenerating. *Aextoxicon punctatum* appears with frequencies of ≥ 50 % in the field and shrub layers of deciduous *Nothofagus obliqua* forests indicating a strong regeneration in the shady understory. The less frequent species, *Lomatia dentata* and *Gevuina avellana,* show similar patterns.
In the zonal primary forests, *Aextoxicon punctatum* has very high frequencies in all layers. *Eucryphia cordifolia* and *Laureliopsis philippiana* are restricted to zonal primary forests and, together with *Aextoxicon punctatum*, form the topmost layer of these stands. *Aextoxicon punctatum* is also the most frequent tree in the extrazonal forests and, together with *Persea lingue*, *Lomatia dentata* and the evergreen *Peumus boldus,* dominates the tree layers of this forest-type. *Persea lingue* and *Laurelia sempervirens* behave differently from the laurophyllous-Valdivian tree species, and we have termed them "laurophyllous-indifferent". Both seem to have a wide ecological amplitude, establishing in insolated sites together with *Nothofagus obliqua*, but showing continuous regeneration in primary forests, normally in small or medium sized gaps. Consequently, we conclude that mixed evergreen-laurophyllous forests are the endpoint of forest succession on undisturbed warmer sites, while pure laurophyllous forests appear to be the "climax" vegetation of zonal stands.
The mean coverage of the tree species in the five forest-types (Figure 4) shows a similar, but much more pronounced, pattern than that in Figure 3. In extrazonal secondary forests the evergreen-mediterranean species have about 20 % coverage, much less than *Nothofagus obliqua* (ca. 60 %), but in the extrazonal primary forests *Nothofagus obliqua* has only 18 % coverage while *Peumus boldus* and *Cryptocarya alba* have a canopy coverage of ca. 25 %. Although the evergreen species have ca. 20 % coverage in the younger secondary forests, the regeneration dynamics of these evergreen species is completely different in the zonal forests where they almost disappear with ongoing succession.
The laurophyllous-Valdivian species start with a coverage of less than 10 % in the extrazonal and zonal secondary forests, but reach absolute dominance (60 %, 120 %) in the respective primary forests with *Aextoxicon punctatum* becoming by far the most important species of old-growth forests. Again the two laurophyllous-indifferent species, *Persea* and *Laurelia,* show less variation, but their coverage maxima in extrazonal primary and tall zonal secondary forests indicate optima under medium shade.
The frequencies of the selected lianas show a similar pattern to those of trees comparing *Nothofagus obliqua* forests with old growth stands (Figure 5). Geophytic and deciduous lianas are widespread in *Nothofagus obliqua* forests, but are almost absent from extrazonal primary forests and completely absent from zonal old growth forests. The introduced deciduous climber *Rubus*

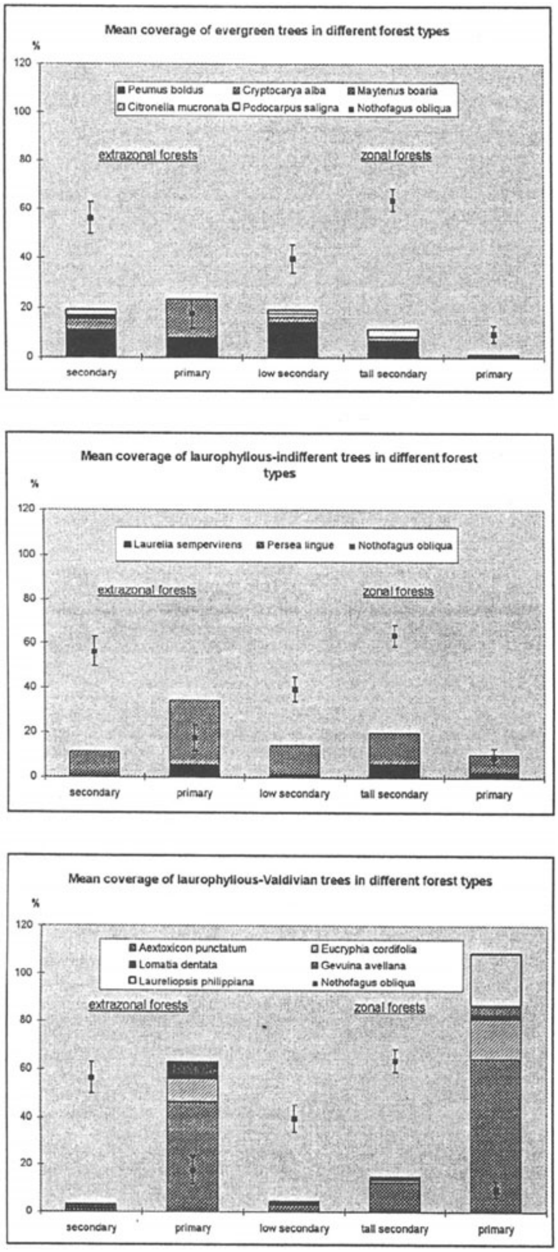

Figure 4: Mean frequency of selected liana species in different forest types

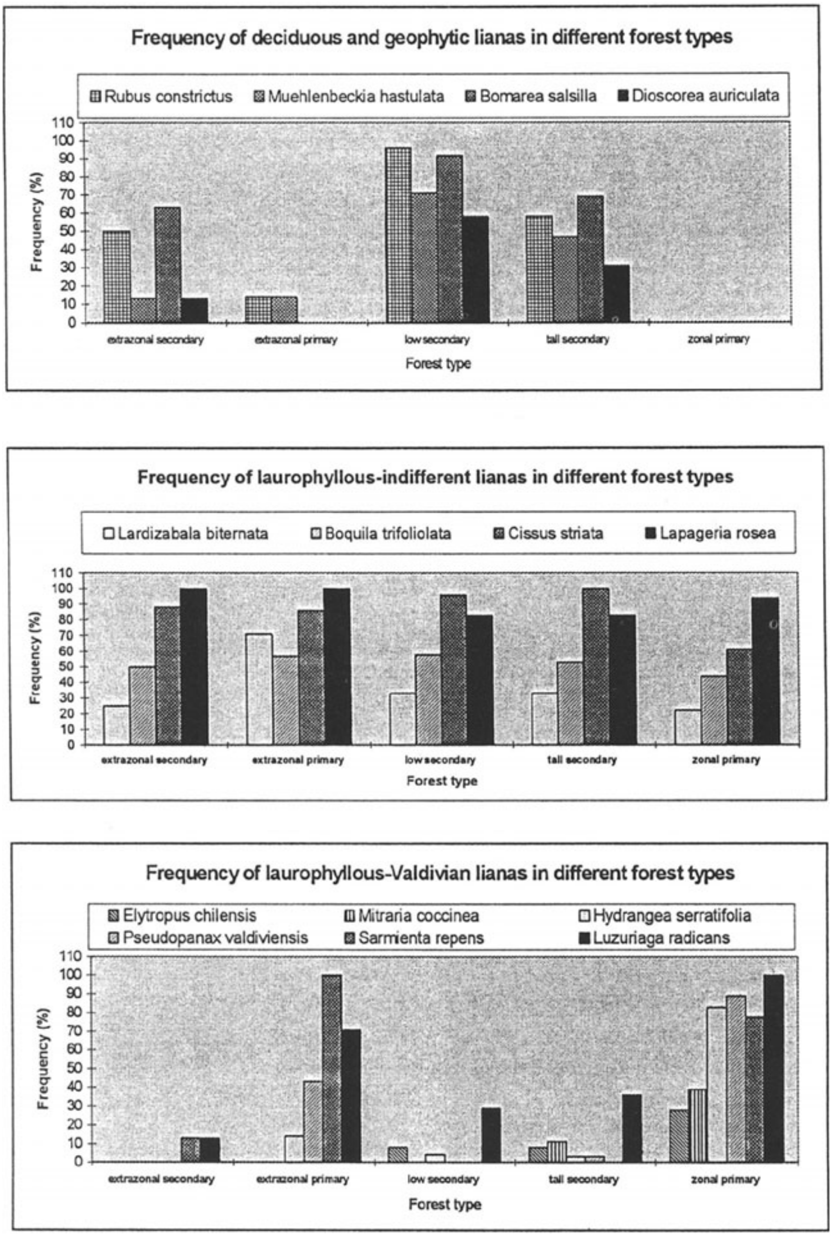

Figure 5: Mean frequency of selected liana species in different forest types

constrictus behaves exactly like the native species *Muehlenbeckia hastulata* and the geophytic vines *Bomarea salsilla* and *Dioscorea auriculata.*
Laurophyllous-indifferent lianas (*Lardizabala biternata*, *Boquila trifoliolata*, *Cissus striata* and *Lapageria rosea*) behave like the laurophyllous indifferent trees: they appear in primary and secondary forests, but with slightly higher frequencies in secondary and extrazonal stands.
The laurophyllous-Valdivian lianas show the opposite pattern, behaving exactly like the laurophyllous-Valdivian trees - with high species numbers and frequencies in zonal primary forests, reduced diversity in intact thermophilous forests and low frequencies or complete absence in secondary forests dominated by *Nothofagus obliqua.*

Discussion

There are few studies of forest dynamics in the ecotonal zone of south central Chile. Veblen et al. (1979) analyzed the stand structure of a similar *Nothofagus obliqua*-dominated old-growth forest in an area with much higher annual precipitation (about 3.000mm) near Villarrica (ca. 40°S). They found no recent regeneration of *Nothofagus obliqua* and continuous regeneration maintaining a steady-state population of *Aextoxicon punctatum*, both observations coinciding with ours in showing laurophyllisation with increasing stand age.
Veblen et al. (1979) found intermittent regeneration of *Persea lingue*, *Eucryphia cordifolia* and *Laurelia sempervirens* and suggested that these species regenerated only in sizeable canopy gaps (30 - 50m^2), although *Persea lingue* (> 10cm dbh) was found to be randomly distributed throughout the stand. Our data show *P. lingue* to be present and regenerating in all vertical strata of old-growth forests (with mean frequencies of 30 - 60 % and > 10 % cover) irrespective of external disturbance. In our study area, *Eucryphia cordifolia* behaves as a late successional species with optimal coverage and ongoing regeneration in old-growth stands. The high number of saplings resulting from abundant root suckering of *Eucryphia* may have biased the results of Veblen et al. (1979) which were based on stem numbers. Nevertheless, like *Aextoxicon punctatum*, these species will be favored in gaps caused by fallen trees.
Our data indicate that *Gevuina avellana* is a late successional species as it attains higher frequencies and coverage only under closed canopies. *Lomatia dentata* is most typical of the main canopy of extrazonal old-growth forests, whereas *Peumus boldus* persists in old-growth forests on zonal sites, and plays an important role on extrazonal sites. The range of both species extends up to the relict *Aextoxicon* forests in the coastal range of North-Central Chile at about 32°S.
The species composition and stand structure of the forest fragments in our study area may be summarized as follows. *Nothofagus obliqua* dominates the

secondary forests, accompanied by evergreen and laurophyllous-indifferent species, whereas in the primary forests different laurophyllous tree species build a closed canopy of 30 - 35m height. Laurophyllous trees of Valdivian origin (e.g. *Aextoxicon punctatum* and *Eucryphia cordifolia*) dominate all vertical strata, indicating favorable conditions for their regeneration. Most of the laurophyllous trees show regeneration patterns typical of shade tolerant late-sucessional species, although *Laurelia sempervirens* and *Persea lingue* show a wide successional amplitude. Evergreen tree species from Central Chile that are near their southern limit in this area show other regeneration patterns. In zonal stands they are most common in earlier succession stages, less frequent in taller secondary forests, and almost absent from the primary forests. In this region, these species originally inhabited extrazonal thermophilous sites with relatively shallow soils. In secondary forests on extrazonal sites, *Nothofagus obliqua* is the first to establish, followed by evergreen trees as *Peumus boldus*, *Cryptocarya alba* and *Citronella mucronata* and, much later, by laurophyllous trees. Intact thermophilous forests have laurophyllous canopies with emergent *Nothofagus obliqua*, a reduced diversity of laurophyllous species, and increased representation of *Lomatia dentata*, *Persea lingue* and *Laurelia sempervirens*. The evergreen trees *Peumus boldus*, and *Cryptocarya alba* form part of the canopy and *Citronella mucronata* survives in the understory with higher frequencies than in the zonal primary forests.

In the study area, any natural reafforestation has followed catastrophic disturbance, typically clear-felling or fires during the last hundred years. In the first post-disturbance period there is a massive cohort establishment of *Nothofagus obliqua* which, after several decades, is typified by a bell-shaped distribution of stem diameters of this tree (Veblen et al. 1979). The establishment of evergreen and (after some delay) laurophyllous tree species occurs after the deciduous canopy is closed, inhibiting the further regeneration of *Nothofagus obliqua* in the understory. Finally, and after long disturbance-free periods, the forest shifts towards a laurophyllous canopy with deciduous emergents - the typical stand structure of the current primary forest fragments. Further absence of disturbance would result in the dominance of *Aextoxicon punctatum* with a considerable admixture of *Persea lingue*, *Laurelia sempervirens*, *Eucryphia cordifolia* and *Laurelia phillippiana* in the main canopy and a high diversity of laurophyllous lianas - i.e. a forest with a structure and species composition typical of the temperate Valdivian rain forests (Gajardo 1994).

The various classifications of the vegetation of southern Chile often disagree about the limits of the different forest types. The "Nothofago-Perseetum lingue" of Oberdorfer (1960) coincides with the mid-successional stages of the "zonal" forests that are widespread in the study area, whereas the thermophilous subassociation, Nothofago-Perseetum boldetosum, corresponds to the mid-successional stages on "extrazonal" sites. Arroyo et al. (1996) excluded our study area from the Valdivian rainforest, assigning the northern limit of this vegetation type in the Central Valley at 41° S. Other authors have also defined individual subareas of deciduous *Nothofagus obliqua* forest in the Central Valley between 40° and 37°S. (Schmithüsen 1956, Quintanilla 1974, Gajardo 1994), despite the fact that most of these forests appear to be anthropogenic and of secondary origin. The zonal old growth forest fragments are dominated by laurophyllous trees, most of them characteristic species of Valdivian rainforests. Laurophyllous lianas and epiphytic ferns contribute to the high species diversity and most of the species have a marked southern temperate (Gondwanan) origin (Finckh 1995). Consequently these forests must be classified as temperate laurophyllous rainforests.

The question as to whether the vegetation shift from deciduous to laurophyllous forests is due to global warming or due to successional processes can be answered only by examining climatic data and the ecophysiology of the trees. Figure 6 shows an annual record (1.7.1996 to 30.6.1997) of monthly maximum and minimum air temperatures measured in the open at a height of 1.5m (means from three stations in the study area).

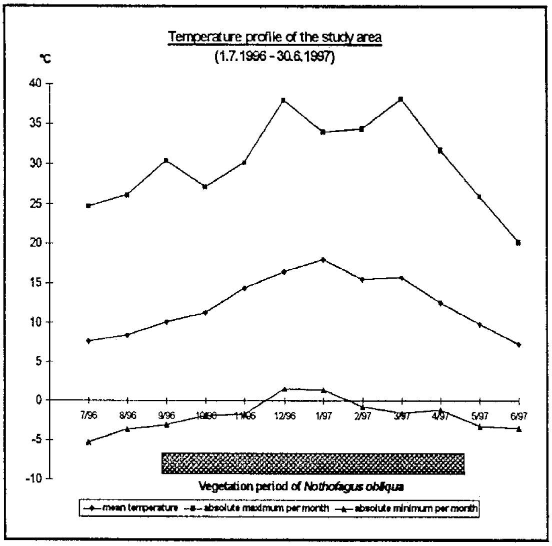

Figure 6: Temperature profile of the study area (1.7.1996 - 30.6.1997)

Maximum temperatures at the soil surface will be considerably greater than those measured at 1.5 m height (up to 40° C). Seedlings of many Valdivian laurophyllous species (e.g. *Eucryphia cordifolia*, *Weinmannia trichosperma* and *Laureliopsis philippiana*) cannot survive heating and the corresponding desiccation (Donoso 1993). Minimum temperatures of < 0°C occurred from February until mid-November (Figure 6). Frosts may occur at any time of year and are frequent from September to mid-November, the early part of growing season. Seedlings of many laurophyllous species are susceptible to frost, especially in late spring, so that it may be difficult for them to establish in the open (Alberdi 1996). In contrast, *Nothofagus obliqua* sprouts vigorously from stumps left after stand destruction. These sprouts are less susceptible to temperature extremes than seedlings and tolerate minimum temperatures down to -15°C (Golte 1983, Read & Brown 1996).

The temperatures in the open are markedly different from those within the stand. Within stands of *Nothofagus obliqua*, the temperature extremes are less pronounced, with lower maxima and higher minima than in the open, outside the stand. After leaf expansion (mid September) and during the whole vegetative period (until the end of April), temperatures within the stand of *Nothofagus obliqua* normally neither exceed 30°C nor fall below 2°C. This amelioration of temperature within stands is well-known and especially significant in regions with frequent frosts and pronounced summer drought, such as the study area. In such conditions, the deciduousness of *Nothofagus obliqua* provides the best strategy for early successional stages (Donoso 1993, Alberdi 1996); neither the seedlings of the evergreen tree species nor those of the laurophyllous trees are able to establish in the open. The sclerophyllous evergreen species appear earlier in the succession than the broad-leaved evergreen trees, but are less adapted to the shaded old-growth conditions in which the Valdivian laurophyllous species find their synecological optimum.

These man-made differences between temperatures in the open and within stands far exceed the changes predicted for global warming. Consequently, the effects of global warming on laurophyllisation are likely to be minor .

Conclusions

Species distribution, vegetation structure and patterns of regeneration in secondary *Nothofagus obliqua* forests and old-growth stands suggest that the laurophyllisation of the *Nothofagus obliqua* forests is a consequence of successional dynamics. After natural or man-made disturbance, especially after forest fires, *Nothofagus obliqua* appears as a pioneer species recolonizing devastated areas. Once the canopy (dominated by *Nothofagus obliqua*) is closed, temperature extremes are less pronounced and the shade tolerant laurophyllous species start to regenerate inside these stands. This process of laurophyllisation further changes the microclimatic conditions, preventing frost in the understory and maintaining high and more stable humidities throughout the year. This is reflected in the appearance of a large number of indicator species associated with high humidity and typical of Valdivian rainforests (e.g. *Hymenophyllaceae*) in the old-growth stands that are now quite scarce in the study area. The current climatic differences between areas in the open and within the stands are much greater than any potential differences due to changes in the global climate.

In the study area, the balance between forests dominated by *Nothofagus obliqua* and those undergoing laurophyllisation depends on the frequency and intensity of man-made fires and other disturbances. Fossil pollen records from the more humid Lakes Region, 400km south of the study area, indicate a continuous incidence of man-made fires since the arrival of the Palaeo-Indians at about 10.000 years B.P. Tree ring analyses from the "primary" Rucamanque forest give us an estimated stand age of about 350 years (A. Vogel, pers. comm.). Huge cleared areas apparently were present at the beginning of the seventeenth century and were subsequently recolonized by forest. Similar stand devastation ca. 300 years ago was described by Lusk (1996) for *Fitzroya cupressoides* forests in Southern Chile. These catastrophic disturbances might be related to the general uprising of the Mapuche Indians against the Spanish colonizers. The use of fire to clear land for agriculture or silviculture increased again during colonization between approx. 1880 and 1940 and is still common in the study area, accounting for forests that are now dominated by *Nothofagus obliqua*. Currently, fire frequency is decreasing due to improved fire control. Cattle grazing in forests and extraction of wood for fuel is frequent among small farmers and wood is still the major domestic fuel for Temuco's 250.000 inhabitants. The intensity and frequency of disturbance regulates the laurophyllisation process - consequently we postulate that the laurophyllisation of these forests is controlled by land-use practice and intensity. Research on laurophyllisation should pay special attention to land-use history and changing land-use patterns and the remaining laurophyllous "climax" forests should be strategic priorities for nature conservation.

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References

Alberdi M. (1996):Ecofisiología de especies lenosas de los bosques higrófilos templados de Chile: Resistencia a la sequía y bajas temperaturas. In: J. Armesto et al. (eds.): Ecología de los Bosques Nativos de Chile, pp. 279-300. Editorial Universitaria, Santiago de Chile.

Arroyo M.T.K. et al. (1996): Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamerica. In: J. Armesto et al. (eds.): Ecología de los Bosques Nativos de Chile, pp. 71-99. Editorial Universitaria, Santiago de Chile.

Berninger O. (1929): Wald und offenes Land in Süd-Chile seit der spanischen Eroberung. Geographische Abhandlungen 3: 1-130. Stuttgart.

Braun-Blanquet J. (1964): Pflanzensoziologie. 3th ed. Springer, Berlin-Wien-New York.

Donoso C. (1993): Bosques templados de Chile y Argentina. Editorial Universitaria, Santiago de Chile.

Finckh M. (1995): Die Wälder des Villarrica-Nationalparks (Südchile) - Lebensgemeinschaften als Basis für ein Schutzkonzept. Dissertationes Botanicae 259. Cramer, Berlin-Stuttgart.

Gajardo R. (1994): Sistema básico de clasificación de la vegetación nativa chilena. Editorial Universitaria, Santiago de Chile.

Golte W. (1983): Verbreitung und ökologische Grundlagen der laubwerfenden *Nothofagus*-Arten im südlichen Andenraum.- In: W. Lauer (ed.) Beiträge zur Geoökologie von Gebirgsräumen in Südamerika und Eurasien, pp. 9-51. Wiesbaden.

Hueck K. (1966): Die Wälder Südamerikas. G. Fischer, Stuttgart.

Lusk C. (1996): Gradient analysis and disturbance history of temperate rain forests of the coast range summit plateau, Valdivia, Chile. Rev. Chil. Hist. Nat. 69: 401-411.

Marticorena C. & Quezada M. (1985): Catálogo de la flora vascular de Chile. Gayana 42: 1-157.

Oberdorfer E. (1960): Pflanzensoziologische Studien in Chile. Flora et Vegetatio Mundi 2. Weinheim/Bergstr.

Quintanilla V. (1974): Les Formations végétales du Chili tempéré.-Doc. de Cartogr. Ecol. 14: 33-80.

Read J. & Brown M. (1996): Ecology of Australian *Nothofagus* Forests. In: T. Veblen et al. (eds.): The Ecology and biogeography of *Nothofagus* Forests, pp. 131-181. Yale University Press, New Haven-London

Schmithüsen J. (1956): Die räumliche Ordnung der chilenischen Vegetation. Bonner geogr. Abh. 17: 1-89.

Schwabe G. (1956): Die ökologischen Jahreszeiten im Klima von Mininco (Chile). Bonner geogr. Abh. 17: 139-182.

Veblen T. T. et al. (1979): Tree regeneration strategies in a lowland *Nothofagus*-dominated forest in south-central Chile. J. of Biogeography 6: 329-340.

Walter H. (1990): Vegetation und Klimazonen. 6th ed. Ulmer, Stuttgart.