Subantarctic forest ecology:

case study of a coniferous–broadleaved stand in Patagonia, Argentina.

Promotoren: Dr.Roelof A.A.Oldeman,
hoogleraar in de Bosteelt & Bosoecologie,
Wageningen Universiteit, Nederland.

Dr.Luis A.Sancholuz,
hoogleraar in de Ecologie,
Universidad Nacional del Comahue, Argentina.

Alejandro Dezzotti

Subantarctic forest ecology: case study of a coniferous-broadleaved stand in Patagonia, Argentina.

PROEFSCHRIFT
ter verkrijging van de graad van doctor
op gezag van de Rector Magnificus
van Wageningen Universiteit
dr.C.M.Karssen
in het openbaar te verdedigen
op woensdag 7 juni 2000
des namiddags te 13:30 uur in de Aula.

Subantarctic forest ecology: case study of a coniferous–broadleaved stand in Patagonia, Argentina

A.Dezzotti. Asentamiento Universitario San Martín de los Andes. Universidad Nacional del Comahue. Pasaje de la Paz 235. 8370 S.M.Andes. Argentina. E–mail: cdezzott@uncoma.edu.ar.

The temperate rainforests of southern South America are dominated by the tree genus *Nothofagus* (Nothofagaceae). In Argentina, at low and mid elevations between 38°–43°S, the mesic southern beech *Nothofagus dombeyi* ("coihue") forms mixed forests with the xeric cypress *Austrocedrus chilensis* ("ciprés", Cupressaceae). A virgin, post–fire stand located on a dry, north–facing slope was examined regarding regeneration, population structures, and stand and tree growth. Inferences on community dynamics were made. Because of its lower density and higher growth rates, *N.dombeyi* constitutes widely spaced, big emergent trees of the stand. In 1860, both tree species began to colonize a heterogeneous site, following a fire that eliminated the original vegetation. This period lasted 60 to 70 years, after which recruitment ceased probably in response to canopy closure that resulted in the present even–aged, clustered adult tree populations. The build–up of the *A.chilensis*–dominated mixed stand probably improved local moisture conditions, encouraging establishment of *N.dombeyi* seedlings, and resulting in the current–day stand structure: a sapling population dominated primarily by *N.dombeyi*, and a mature overstorey dominated primarily by *A.chilensis*. Due to the differences in abundance and growth of the regeneration between both species, *N.dombeyi* is expected to gradually become dominant or even completely replace *A.chilensis*. However, in the conifer the combination of a great longevity and a light–demanding temperament implies that frequent to very infrequent large–scale impacts would be sufficient to maintain its abundance in the site. These results, together with others described in literature, suggest that divergent development patterns occur in *A.chilensis–N.dombeyi* mixed stands, probably because these forests grow under a spatially varied environment and their responses vary consequently.

Published by the author.

ISBN 90-5808-216-4
Printed by Van Gils Grafisch Service Centrum, Wageningen, Nederland.

PROPOSITIONS

attached to the doctoral thesis

"Subantarctic forest ecology: case study of a coniferous–broadleaved stand in Patagonia, Argentina",

by

Alejandro Dezzotti.

1) Although in overlapping parts of their territories *Nothofagus dombeyi* and *Austrocedrus chilensis* co–exist in the same sites, there is a clear niche differentiation in space and time between both species as a result of their contrasting life–histories. (This thesis).
2) Conceptual models of the successional dynamics of *Nothofagus*–dominated forests of the high–latitude region of South America are essential to prevent and correct vegetation management problems. (This thesis).
3) "The rate of resource use is ultimately a social and economic decision within certain biological and physical constraints, so technical aspects of change in management practices do not accomplish the difficult task of deciding the balance between competing management objectives and value systems". FJ Swanson & JF Franklin. 1992. Ecological Applications 2(3): 262–274.
4) Despite the impressive scientific progress in products, the fundamental contribution of science to humankind is a philosophical position opposed to the search for absolute and permanent truth.
5) Whereas *Pinguinus impennis* required millennia of complex and unknown processes to become a penguin of the northern Atlantic, on June 4, 1844, one person destroyed the last two individuals and the last egg in Iceland in a matter of minutes, leaving us poorer for eternity.
6) During the last three million years mankind has broken up the boundaries imposed by the physical environment and colonised the planet without breaking up, however, the limits of its own cultural and religious prejudices.
7) Each kind of monera, protist, fungus, plant, and animal has many very closely related species, *Homo sapiens* being the unique exception to this rule, a discrepancy the causes of which are insufficiently known and yet are elements essential to our knowledge.
8) The fundamental answer to the question of why we must preserve biodiversity is not scientific but ethical.
9) The general problem with definitions is well exemplified by "tree", a noun whose meaning can not be sharply defined.
10) The language of the *Athshian* people of Ursula K.LeGuin (1972) is right when designating "world" and "forest" by the same word.

Wageningen, June 7th, 2000

The word for world is forest.

Ursula K.Le Guin (1972).

With love and gratitude
to the memory of Claudio and Luis Dezzotti,
to Ilse, Marisol, and Luciana,
and to my friends.

Content

Abstract 7

Resumen 10

Samenvatting 13

1. Introduction 16
    - Plant ecology and vegetation management 16
    - The *Austrocedrus-Nothofagus* forests 17
    - Objectives 18

2. Angiosperms and gymnosperms 20
    - Evolutionary trends 20
    - Longevity and growth 24
    - Juvenile growth 28

3. The biome 33
    - Climate 33
    - Geological setting 35
    - Floristic composition 37
    - Vegetation types 41
    - Soils 47
    - Quaternary history 48
    - Ecological impacts 50

4. The species 53
    - Origin and diversification 53
    - Biology and distribution 56
    - Species and forest dynamics 58

5. The *Austrocedrus-Nothofagus* stand 68
    - Methodology 68
        - Size and age structures 68
        - Spatial structure 70
        - Stand and tree growth 73
        - Minimum area 74
    - Stand patterns and processes: results and discussion 76
        - Site characteristics 76
        - Stand structure 80
            - Performance structure 80
            - Age structure 86
            - Spatial structure 88
        - Growth and interaction 91
            - Rationale 92
            - Results 96
        - Growth and reproduction 98
            - Rationale 98
            - Results 104
        - Stand dynamics 106
    - Minimum area 111
        - Rationale 112
        - Results 113

6. Conclusions 116
    - Stand and tree growth 116
    - Growth and dioecy 119
    - Stand development 121
    - Minimum area 123

References 125

Acknowledgments 140

Abstract

In the temperate rainforests of southern South America, the tree genus *Nothofagus* (Nothofagaceae) is the dominant one in extension and abundance on zonal soils at different latitudes and altitudes, as well as on intrazonal soils (e.g., wetlands) and azonal soils (e.g., morrenic and fluvioglacial deposits). Although great concern as to the global role of this biome is expressed today, the existing level of ecological knowledge of its functioning is still inadequate to design sound management to maintain or enhance forest values, services, and commodities. Vegetation misuse triggers severe biotic and physical deterioration, particularly in the intrinsically fragile Andean Patagonic region characterised by seasons with high rainfall levels, low temperature, strong intensity and frequency of winds, and extensive and deep mountain slopes. In Argentina, at low– and mid–elevations between 38° and 43°S and the annual isohyets of 1,500 to 2,000mm, the forest is mixed and composed of the xeric cypress *Austrocedrus chilensis* ("ciprés", Cupressaceae) and the mesic southern beech *Nothofagus dombeyi* ("coihue"). The strong east – west environmental gradient caused by the effect of the rain–shadow of the Andes on community composition and dynamics is striking. This is reflected in a clear vegetational zonation, bordered by the sparse *A.chilensis* woodland surrounded by the Patagonian steppe towards the east and the Valdivian rainforest co–dominated by *N.dombeyi* towards the west. Both communities are separated only by tens of kilometres. The conifer–angiosperm association, characterised by two groups of plants with contrasting evolutionary histories and ecological adaptations, has received little scientific attention.

At 41°11'S and 71°25'W, a mixed, virgin, post–fire stand, located on a dry north–facing slope was examined as to regeneration, size, age, and spatial structures, and stand and tree growth. Inferences on community dynamics were made. The minimum area of the community was also estimated. Density, basal area, and volume of adult trees were calculated to be 658 ind ha^{-1} (66.6% of *A.chilensis*), 72.1 m^{2}ha^{-1} (65.6%), and 608.7m^{3}ha^{-1} (51.2%), respectively. Total density of saplings and seedlings is 2,991 (27.1% of *A.chilensis*) and 7,143 ind ha^{-1} (34.3%), respectively. Stand growth was estimated to be 7.3m^{3}ha^{-1}yr^{-1} (42.5% of *A.chilensis*) and 3.7 t ha^{-1}yr^{-1} (32.4%). Between species, individual increments significantly differ within development stages. Adult *A.chilensis* and *N.dombeyi* show an individual diameter increment of 0.36 and 0.57cm yr^{-1}, respectively, and a height increment of 15.8 and 29.3cm yr^{-1}, respectively. Saplings of *A.chilensis* and *N.dombeyi* grow in diameter at a rate of 0.11 and 0.21cm yr^{-1}, respectively, while their height increases at a rate of 7.8 and 17.2cm yr^{-1}, respectively. Within species, adults grow in diameter at rates between 2.7 (in *N.dombeyi*) and 3.2 (in *A.chilensis*) times significantly faster than their respective saplings, and also old trees show significantly larger diameter increments than young trees. Within species, adults grow in height at rates between 0 (in *N.dombeyi*) and 2.0 (in *A.chilensis*) times faster than their respective saplings. In *A.chilensis,* old trees grow in height at significantly higher rates than young trees, whereas this is not the case for *N.dombeyi*. For each *A.chilensis* tree, a negative relationship is found between individual diameter (range= 0.22 to 0.42cm yr^{-1}) and height growth (12 to 21cm yr^{-1}), and the number of neighbouring trees (0 to ≥7) taller than itself within a 5m distance. Contrarily, for *N.dombeyi* no relationship is observed between these variables. In *A.chilensis*, individual growth rates do not differ significantly between sex classes: for males, mean and current diameter, and height growth rate being 0.360, 0.132, and

17.6cm yr^{-1}, respectively, while for females they are 0.348, 0.124, and 17.2cm yr^{-1}, respectively.

The inherently inferior growth capacity of *A.chilensis* over *N.dombeyi* is explained by its lower rate of leaf photosynthesis. Conifers from the northern hemisphere show a primary productivity similar to their mostly associated deciduous angiosperms. However, conifers from the southern hemisphere show a lower productivity than their broadleaved associates. This is probably due to their incapacity to benefit differentially from an extended period of net photosynthesis as they co–exist mainly with broadleaved evergreen species. The greater growth disadvantage of *A.chilensis* in comparison to *N.dombeyi* during the juvenile stage is consistent with the same trend observed in gymnosperms as a group: the seedling represents the ontogenetic phase of slowest growth, caused by multiple factors related to leaf productivity and carbohydrate allocation. This constraint has been used to explain the decline and retreat of gymnosperms along evolutionary scales. Within species, the dependence of growth on age and crowding is indicative of one–sided, asymmetric position in the light: trees that arrived earlier to the site have used the resources to develop a larger size, and therefore at present they interfere asymmetrically with those arriving later. Contrasting responses to these light conditions are found according to species and growth variables: i) In *N.dombeyi*, the independence of individual growth to crowding, and of height growth to age / development stage of trees suggests that this species has a rather large interval of shade tolerance. On the contrary, *A.chilensis* is highly susceptible to shade effects judging from the dependence between growth, age, and taller neighbours. ii) In comparison to diameter growth, height growth differs slightly between age classes / stages, which reflect the priority that trees commonly give to height during development. Lack of sex–related growth differences in the dioecious *A.chilensis* would be masked by the low reproductive development exhibited in the sampled individuals. If trees in a structurally well–developed stand are unable to express the same reproductive potential as observed in isolated trees, then its incidence on the individual energy budget would be marginal and marked intersexual growth contrasts would not be expected. This hypothesis would explain the incongruence with previously results suggesting a trade–off between vegetative and reproductive investments. It still needs to be confirmed by future studies given, also given the ecological and silvicultural relevance of this issue.

In 1860, both tree species began to colonize a heterogeneous site, following a fire that eliminated the original vegetation. This first regenerative pulse lasted 60 to 70 years, after which recruitment ceased probably in response to canopy closure, resulting in the present even–aged clustered adult tree populations. Because of its lower density and higher growth rates, *N.dombeyi* exists as widely spaced, big emergent trees throughout the stand. The build–up of the mixed stand dominated by *A.chilensis* probably improved local moisture conditions autogenously, encouraging the establishment of *N.dombeyi* seedlings and defining a second continuous regenerative pulse starting around1930. In the understorey, the sapling population dominated by *N.dombeyi* represents a third regenerative pulse with ages between 1 and 10 years. The current–day stand structure is represented by a young population dominated primarily by *N.dombeyi*, and a mature overstorey dominated primarily by *A.chilensis*. In the absence of large–scale impacts, changes in forest structure over time would be accounted for by interspecific differences in recruitment, growth rate, and sensitivity to competition, probably resulting in a local decline of the conifer component. However, the combination of a great longevity and a light–demanding temperament of *A.chilensis* implies that frequent to very infrequent

large–scale impacts would be sufficient to maintain its abundance in the landscape. These results, together with others described in literature, suggest that divergent development patterns occur in the *A.chilensis* – *N.dombeyi* stands, probably because these forests grow under a spatially varied environment and their responses differ consequently.

Based on the concept of "quantitative minimum area", the statistically optimum plot size for the ecological study of a temperate forest was examined. Changes in the estimated tree density (N), basal area (G), stemwood volume (V), and volume growth rate (I_V) per area unit, in relation to the increase of sample plot size (X), were analysed. Means of N, G, V, and I_V fluctuated considerably within a range of small plot sizes, showing stability at $X \geq 1{,}000 m^2$. The accuracy of the parameters estimates, calculated as relative error (RE), increases as long as the plot size is enlarged. For $X = 1{,}000 m^2$, ER varies between ± 30% and ± 49%, and for $X = 2{,}500 m^2$, RE varies between ± 20% and ± 32%. Around $X = 5{,}000 m^2$ should be sampled to obtain $RE \leq \pm 20\%$ in all variables, according to the developed regressions $RE = f(X)$ ($P<0.05$). This estimated plot size is larger than those often recommended in literature for ecological studies of temperate forests.

Keywords: *Austrocedrus chilensis* – *Nothofagus dombeyi* – Population structures – Stand growth – Competition– Stand development – Sexual dimorphism – Minimum area.

Nomenclature: Correa (1969–1985).

Ecología de los bosques subantárticos: estudio de caso de un rodal de coníferas y latifoliadas en la Patagonia, Argentina.

Resumen

En los bosques pluviales templados del sur de Sudamérica, *Nothofagus* (Nothofagaceae) es el género arbóreo dominante en extensión y abundancia tanto sobre los suelos zonales en diferentes latitudes y altitudes, como sobre los intrazonales (e.g., mallines) y azonales (e.g., morrenas y depósitos fluvioglaciales). El conocimiento científico sobre el funcionamiento de este bioma es todavía inadecuado para diseñar sistemas de manejo sustentables que preserven en el largo plazo los valores, bienes y servicios esenciales que provee. Esta estrategia es esencial en la intrínsecamente frágil Patagonia andina, caracterizada por altos niveles de precipitación estacional, bajas temperaturas, fuertes e intensos vientos, y extensas y pronunciadas pendientes. En la Argentina, a bajas e intermedias altitudes, entre los 38° y 43° lat.S. y las isohietas anuales de 1.500 y 2.000mm, el bosque está compuesto por la especie xérica *Austrocedrus chilensis* ("ciprés", Cupressaceae) y la mésica *Nothofagus dombeyi* ("coihue"). El marcado gradiente ambiental este–oeste causado por la "sombra de lluvias" de los Andes influye en forma marcada sobre la composición y dinámica de estos bosques. Esto se refleja en una zonación vegetal cuyos extremos son los bosquetes abiertos de *A.chilensis* rodeados por la estepa patagónica hacia el este, y la selva valdiviana co–dominada por *N.dombeyi* hacia el oeste, separados sólo por unas decenas de kilómetros.

Un rodal virgen, maduro, post–fuego, dominado por *A.chilensis* y *N.dombeyi*, localizado a los 41°11'lat.S. y 71°25' long.O., se examinó con relación a la estructura, el crecimiento y la sucesión. Adicionalmente, se estimó el área mínima de la comunidad. La densidad, el área basal y el volumen de árboles adultos son 658 ind ha^{-1} (66,6% de *A.chilensis*), 72,1 m^{2}ha^{-1} (65,6%) y 608,7m^{3}ha^{-1} (51,2%), respectivamente. La densidad de juveniles y plantines es 2.991 (27,1% de *A.chilensis*) y 7.143 ind ha^{-1} (34,3%), respectivamente. El crecimiento de madera se estimó en 7,3m^{3}ha^{-1}año^{-1} (42,5% de *A.chilensis*) y 3,7 t ha^{-1}año^{-1} (32,4%). Los adultos de *A.chilensis* y *N.dombeyi* crecen en diámetro a una tasa individual de 0,36 y 0,57cm año^{-1}, respectivamente, mientras que en altura a 15,8 y 29,3cm año^{-1}, respectivamente. Los juveniles de *A.chilensis* y *N.dombeyi* crecen en diámetro a una velocidad de 0,11 y 0,21cm año^{-1}, respectivamente, mientras que en altura a una de 7,8 y 17,2cm año^{-1}, respectivamente. El incremento de los individuos difiere significativamente entre especies. Los adultos crecen en diámetro a una tasa entre 2,7 (en *N.dombeyi*) y 3,2 (en *A.chilensis*) veces más rápida que sus respectivos juveniles, y los árboles más viejos expresan incrementos superiores a los más jóvenes. Los adultos crecen en altura a una tasa entre 0 (en *N.dombeyi*) y 2,0 (en *A.chilensis*) veces más rápida que sus respectivos juveniles. En *A.chilensis*, los árboles de mayor edad crecen en altura a velocidades más rápidas que aquellos de menor edad, mientras que en *N.dombeyi* se observa una relación independiente entre esas variables. Para cada *A.chilensis*, se encuentra una dependencia negativa entre el crecimiento individual en diámetro (rango = 0.22 y 0.42cm año^{-1}) y altura (12 – 21cm año^{-1}), y el número de vecinos más altos que el árbol objeto en un radio de 5m. Contrariamente, en *N.dombeyi* se observa independencia entre esas variables. En la especie dioica *A.chilensis*, las tasas de crecimiento individuales no difieren en forma significativa entre clases de sexo: en los

machos, el incremento medio y corriente en diámetro, y en altura es 0,360, 0,132 y 17,6cm año^{-1}, respectivamente, mientras que en las hembras es 0,348, 0,124 y 17,2cm año^{-1}, respectivamente.

La capacidad de crecimiento intrínsecamente inferior de *A.chilensis* se debería a su menor tasa de fotosíntesis. Las coníferas del hemisferio norte exhiben una productividad equivalente a la de las angiospermas deciduas con las que comparten los sitios. En cambio, las coníferas del hemisferio sur presentan una productividad menor a las angiospermas arborescentes, probablemente porque no se benefician en forma diferencial de un período extendido de fotosíntesis ya que co–existen habitualmente con especies perennes. En los juveniles de *A.chilensis*, la mayor desventaja del crecimiento en relación con *N.dombeyi* es consistente con la tendencia observada en las gimnospermas: los juveniles representan la fase ontogénica de menor crecimiento, debido a factores vinculados a la fotosíntesis y a la inversión en órganos asimilatorios. Esta limitación se ha utilizado para explicar el retroceso del taxón observado a lo largo de escalas evolutivas. La dependencia entre el crecimiento individual y la edad y la abundancia de árboles vecinos indica el efecto de la competencia asimétrica por luz: los árboles que arribaron tempranamente al sitio habrían aprovechado anticipadamente los recursos y adquirido un mayor tamaño, y en consecuencia interfieren asimétricamente con aquellos que se establecieron más tarde. Sin embargo, ocurren respuestas diferentes de acuerdo a las especies y a las variables: i) En *N.dombeyi*, la independencia entre el crecimiento y la cantidad de vecinos más altos y entre el crecimiento en altura y la edad / estadio sugiere su relativa insensibilidad a la competencia. En *A.chilensis*, la dependencia negativa entre el crecimiento y la edad y la presencia de vecinos indica que su mayor susceptibilidad a la competencia. ii) La diferencia menos marcada del crecimiento en altura en comparación con el del diámetro entre clases de edad / estadios de desarrollo, indica que los árboles dan prioridad a la primera dimensión sobre la segunda; esta tendencia es general en los árboles. En *A.chilensis*, la ausencia de diferencias en el crecimiento entre sexos estaría enmascarada por el escaso desarrollo reproductivo de los individuos muestreados: si en rodales estructuralmente más complejos los árboles son incapaces de expresar el potencial reproductivo que sí se observa en individuos aislados, su incidencia sobre el presupuesto energético sería marginal y entonces no se esperarían diferencias sustanciales de crecimiento entre sexos. Esta hipótesis explicaría la incongruencia con resultados presentados en forma previa que sugieren un intercambio entre la inversión vegetativa y la reproductiva en *Austrocedrus chilensis*, y se la debería poner a prueba dada la relevancia ecológica y silvicultural del tema.

En 1860, las especies arborescentes comenzaron a colonizar un sitio heterogéneo, luego de la eliminación de la vegetación original causada por un incendio. Este primer pulso de regeneración dominado por *A.chilensis* se extendió alrededor de entre 60 y 70 años, después el reclutamiento cesó probablemente en respuesta al cierre de la canopia resultando en las actuales poblaciones coetáneas y agrupadas. *N.dombeyi* está representado por árboles aislados, emergentes y de gran tamaño debido a su baja densidad y mayor tasa de crecimiento. El desarrollo del rodal habría provocado un mejoramiento autogénico de las condiciones de humedad, promoviendo el establecimiento de *N.dombeyi* que define un segundo pulso de regeneración. En el sotobosque, la cohorte de juveniles dominada por *N.dombeyi* representa un tercer pulso de regeneración. En ausencia de perturbaciones ecológicas de gran escala, se esperan cambios en la estructura del bosque a lo largo del tiempo influidos por las

diferencias interespecíficas en relación con el reclutamiento, el crecimiento, y la capacidad competitiva, resultando en una disminución local de *A.chilensis.* Sin embargo, la combinación de una extendida longevidad e intolerancia a la sombra implica que disturbios desde muy frecuentes hasta muy infrecuentes serían suficientes para mantener su abundancia en el sitio. Los resultados presentados aquí junto con aquellos reportados en forma previa, sugieren que secuencias sucesionales divergentes ocurren en estos bosques mixtos, probablemente debido a la presencia de un ambiente que cambia espacialmente en forma pronunciada, y entonces las respuestas de la vegetación varían consecuentemente.

Basado en el concepto de "área mínima cuantitativa", se estimó el tamaño estadísticamente óptimo de una parcela de muestreo para el estudio de este bosque templado. Se analizaron los cambios de la densidad, el área basal, el volumen de madera y el crecimiento volumétrico del rodal, en relación con el aumento del área (X) utilizada para estimar tales parámetros. La media de los parámetros fluctuó considerablemente dentro de un rango de tamaños de parcela pequeños, y se estabilizan a partir de $X \geq 1.000 m^2$. La precisión de las estimaciones de las variables, medida en términos del error relativo (ER), se incrementó al aumentar X. Para $X = 1.000 m^2$, ER varió entre ± 30% y ± 49%, y para $X = 2.500 m^2$, ER varió entre ±20% y ±32%. Utilizando regresiones $ER = f(X)$ ($P<0,05$), se estimó que se debería muestrear al menos $X = 5.000 m^2$ para obtener $ER \leq \pm 20\%$ en todas las variables. En general, esta área estimada de muestreo es mayor que las sugeridas por otros autores para el estudio de la ecología de bosques templados.

Palabras clave: *Austrocedrus chilensis* – *Nothofagus dombeyi* – Estructuras de población – Crecimiento – Competencia – Sucesión ecológica – Dimorfismo sexual – Area mínima.

Nomenclatura: Correa (1969–1985).

Subantarctische bosecologie: aan een gemengd bos met naald- en loofbomen in Patagonië, Argentinië.

Samenvatting

In de gematigde streken van zuidelijk Zuid-Amerika is het genus *Nothofagus* (Nothofagaceae) ofwel de beuk van het zuidelijk halfrond, de meest dominante boomsoort, zowel in verspreiding als in aantal. Hij komt voor op bodems die onder invloed van het klimaat gevormd zijn over vele breedtegraden en verschillende hoogten, alsook op de anaërobe intrazonale en jonge azonale bodems (morenen en fluvioglaciale afzettingen). Hoewel de bezorgdheid over de processen die zich in het gebied voltrekken momenteel algemeen is, is het bestaande niveau van ecologische kennis nog onvoldoende om een gezond beheer te ontwikkelen. Verkeerd gebruik van de vegetatie kan onherstelbare schade aanrichten aan het ecosysteem, met name in dit kwetsbare Andes-Patagonië gebied dat gekenmerkt wordt door seizoensgebonden hoge neerslag, lage temperatuur, veel wind en een sterk reliëf. Het bos in dit laag- en middelgebergte van Argentinië, gelegen tussen 38° en 43°ZB en met een jaarlijkse neerslag tussen de 1500 en 2000mm, is samengesteld uit de droogteminnende cypres *Austrocedrus chilensis* ("ciprés", Cupressaceae) en de vochtminnende zuidelijke beuk *Nothofagus dombeyi* ("coihue"). Het Andes gebergte heeft grote invloed op de klimatologische omstandigheden waarin deze boomsoorten groeien. Dit uit zich in grote klimatologische verschillen over kleine afstanden, als gevolg van regenschaduw en hoogteverschillen, en veroorzaakt een sterke oost-west gradiënt in het gebied. Dit weerspiegelt zich in een vegetatie-zonering met als uitersten het pure *A.chilensis* woud omgeven door de Patagonische steppe in het oosten en het Valdivische regenwoud, dat mede gedomineerd wordt door *N.dombeyi,* in het westen. Deze twee uitersten liggen slechts enkele tientallen kilometers van elkaar. Dit ecosysteem dat gekenmerkt wordt door twee groepen van planten waarvan de evolutionaire geschiedenis en ecologische aanpassing onderling zeer contrasteren, heeft nog weinig wetenschappelijke aandacht gehad.

Op 41°11'ZB en 71°25'WL werd een *A.chilensis* – *N.dombeyi* opstand onderzocht. Deze op een droge noordhelling gelegen opstand, was spontaan ontstaan na een bosbrand. Het onderzoek richtte zich op regeneratie, omvang, leeftijd en ruimtelijke structuur alsmede op de groei van de opstand in zijn geheel, zowel als die van de individuele boom. Uiteindelijk werden er conclusies getrokken aangaande de dynamiek in deze ecologische eenheid. Daarnaast werd het minimaal vereiste oppervlak van de ecologische eenheid geanalyseerd. Dichtheid, stamoppervlak en het volume van de volwassen bomen werden geschat: 658 individuen ha^{-1} (66,6% *A.chilensis*), 72,1m^2 ha^{-1} (65,6%), en 608,7m^{3}ha^{-1} (51,2%). De totale dichtheid van zaailingen en jonge bomen bedroeg respectievelijk 2.991 (27,1% *A.chilensis*) en 7.143 individuen ha^{-1} (34,3%). De aanwas werd geschat op 7,3m^{3}ha^{-1}j^{-1} (42,5% *A.chilensis*) en 3,7 t ha^{-1}j^{-1} (32,4%). De verschillen in aanwas tussen individuën van beide soorten waren aanzienlijk voor alle ontwikkelingsstadia. Volwassen *A.chilensis* en *N.dombeyi* vertonen en diameter-aanwas van respectievelijk 0,36 en 0,57cm j^{-1} en een hoogte-aanwas van respectievelijk 15,8 en 29,3cm j^{-1}. Jonge *A.chilensis* en *N.dombeyi* bomen hebben een diameter-aanwas van, respectievelijk, 0,11 en 0,21cm j^{-1} en een hoogte-aanwas van respectievelijk 7,8 en 17,2cm j^{-1}. Binnen een soort is de diameter-aanwas van volwassen bomen tussen 2,7 (in *N.dombeyi*) en 3,2 (in *A.chilensis*) maal sneller dan bij

hun jonge soortgenoten. Bovendien geven oudere bomen een significant snellere groei in diameter te zien. Bij *A.chilensis* is de hoogte–groei van de oudere boom aanzienlijk sneller dan van de jonge, hetgeen bij *N.dombeyi* niet het geval is. De hoogte–aanwas is bij de volwassen bomen tussen de 0 (in *N.dombeyi*) en 2,0 (in *A.chilensis)* maal zo groot als bij hun jongere soortgenoten. Voor elke *A.chilensis* boom werden negatieve relaties gevonden tussen zowel de diameter–toename (0,22 tot 0,42cm j^{-1}) als de hoogte–groei (12 tot 21cm j^{-1}), en het aantal omringende bomen groter dan die boom (0 tot ≥7 binnen 5m). Voor *N.dombeyi* werd daarentegen geen relatie waargenomen tussen deze variabelen. Bij *A.chilensis*, verschillen de groeicijfers niet significant tussen de seksen: bij de mannelijke bomen was de gemiddelde diameter–aanwas, respectievelijk de dikterogroei over de laatste 20 jaar 0,360 en 0,132cm j^{-1}. De hoogtegroei bedroeg 17,6cm j^{-1}. Voor de vrouwelijke bomen was dit respectievelijk 0,348, 0,124, en 17,2cm j^{-1}.

De lagere groeicapaciteit van *A.chilensis* ten opzichte van *N.dombeyi* kan verklaard worden door de lagere fotosynthese van het blad. Coniferen van het noordelijk halfrond tonen een primaire productiviteit die lijkt op die van de bladverliezende angiospermen waarmee ze samenleven. De coniferen van het zuidelijk halfrond daarentegen, tonen een beduidend lagere productiviteit dan de loofbomen. Dit komt waarschijnlijk omdat ze samenleven met groenblijvende loofhout soorten. Bij jonge bomen klopt de grotere groeiachterstand die bij *A.chilensis* is waargenomen ten opzichte van *N.dombeyi* met de tendens zoals die is waargenomen bij de gymnospermen als groep: zaailingen vertegenwoordigen de langzaamste groei tijdens de orthogenetische fase bij deze groep planten. Dit wordt veroorzaakt door meerdere factoren die verband houden met bladproductiviteit en verdeling van koolwaterstoffen. Uit deze beperking verklaart men de afname van het aantal en de terugtocht van de gymnospermen in termen van de evolutie. Binnen de soorten is de afhankelijkheid van groei van de leeftijd en populatie dichtheid een maat voor de eenzijdige asymmetrische competitie: de bomen die als eerste op een plaats voorkwamen hebben de grondstoffen ook als eerste ter beschikking. Met name geldt dit voor licht dat zij, door hun voorsprong in omvang, als eerste kunnen onderscheppen, zodat zij asymmetrisch invloed hebben op de bomen die later komen. Er zijn echter verschillende reacties waargenomen samenhangende met de soort en met groei–variabelen. i) De onafhankelijkheid van individuele groei van de populatie dichtheid en die van de hoogte–groei van leeftijdsklasse en ontwikkelingsfase zijn aanwijzingen dat *N.dombeyi* nogal ongevoelig is voor de asymmetrische competitie. Daarentegen is *A.chilensis* zeer gevoelig, geoordeeld naar de onderlinge afhankelijkheid tussen zowel groei als leeftijd van het aantal grotere buren. ii) In vergelijking met de diameter–groei verschilt de hoogte–groei erg weinig tussen leeftijdsklasse en ontwikkelingsfase. Dit geeft de algemene prioriteit weer, die de bomen aan hoogte–groei geven. De afwezigheid van geslachtsgerelateerde groeiverschillen bij de tweeslachtige *A.chilensis* zou verklaard kunnen worden uit de lage reproductie die bij de bemonsterde individuen is waargenomen. Als de bomen in deze goed ontwikkelde bossen minder reproductie–potentieel laten zien dan dat wat bij meer geïsoleerde bomen is waargenomen, dan zou ook de aanslag door de reproductie op het individuele energiebudget marginaal zijn, waardoor geen belangrijke verschillen in groei tussen de seksen verwacht worden. Deze hypothese, die de incongruentie met voorgaande onderzoeken zou verklaren, suggereert een uitruil tussen de vegetatieve en de reproductieve investeringen en moet verder worden getest in toekomstige studies, gezien de ecologische en bosbouwkundige betekenis van dit onderwerp.

In 1860 begonnen beide soorten met het koloniseren van een heterogene groeiplaats, nadat de oorspronkelijke vegetatie was verbrand. Deze eerste aanzet van de verjonging duurde 60 tot 70 jaar waarna dit proces stopte, waarschijnlijk als gevolg van sluiting van het kronendak. Dit resulteerde in de huidige eenzijdige leeftijdsopbouw van deze sterk geclusterde bomenpopulatie. Vanwege de lagere dichtheid en hogere groeisnelheid staat de *N.dombeyi* geïsoleerd en is erg groot. De opbouw van de door *A.chilensis* gedomineerde gemengde opstand verbeterde waarschijnlijk de vochttoestand, waardoor de installatie van *N.dombeyi* werd aangemoedigd en er een tweede verjongingsproces werd geïnitialiseerd in de jaren'dertig. Een derde factor die de verjonging positief beïnvloedt is de dominante aanwezigheid van *N.dombeyi* in de populatie zaailingen. De hedendaagse opstand wordt vertegenwoordigd door een jonge populatie, hoofdzakelijk gedomineerd door *N.dombeyi*, met daarboven een volwassen bovenlaag waar *A.chilensis* domineert. Bij afwezigheid van grote externe invloeden worden veranderingen in bosstructuur veroorzaakt door verschil in verjongings–vermogen tussen beide soorten, zowel als verschil in groeisnelheid en negatieve interactie tussen de soorten. Hierdoor zal het coniferengehalte van dit bos waarschijnlijk iets afnemen. De combinatie van hoge lichteisen en lange levensduur veronderstelt dat grootschalige, frequente tot zeer frequente omgeringskrachten een overvloed van *A.chilensis* in het landschap zal bevorderen. Samen met andere in de literatuur beschreven resultaten suggereren deze resultaten dat divergente ontwikkelingspatronen optreden in de gemengde *A.chilensis* – *N.dombeyi* opstand, waarschijnlijk omdat deze bossen in een ruimtelijk gevarieerde omgeving voorkomen waarop de respons der boomsoorten verschillend is.

Op basis van het concept van het "kwantitatief minimum oppervlak" is de statistisch optimale eenheid voor ecologische studie van een gematigd bos, onderzocht. Er werd een analyse uitgevoerd naar de veranderingen in geschat stamtal (N), grondvlak (G), volume–aanwas (V) en de volumegroeisnelheid (I_V) in relatie tot de toename van het bestudeerde landoppervlak (X). De gemiddelde waarden van N, G, V en I_V fluctueerden aanzienlijk bij kleine oppervlakten en toonden stabiliteit bij $X \geq 1.000m^2$. De nauwkeurigheid van de geschatte parameters, berekend als relatieve fout (RE), neemt toe bij toenemende oppervlak. Voor $X= 1.000m^2$ varieert RE tussen ± 30% en ± 49% en voor $X= 2.500m^2$ varieert RE van ± 20% tot ± 32%. Bij een ecologische eenheid van $X= 5.000m^2$ verkrijgen we waarden van $RE \leq \pm 20\%$ in alle variabelen, volgens de gebruikte regressie analyse $RE= f(X)$ ($P<0{,}05$). Deze geschatte oppervlakte is groter dan meestal wordt aangegeven in aanbevolen literatuur voor ecologische onderzoeken van gematigde bossen.

Trefwoorden: *Austrocedrus chilensis* – *Nothofagus dombeyi* – Populatie structuur – Opstandsaanwas – Competitie – Opstandsontwikkeling – Sexuele dimorfisme – Minimaal oppervlak.

Nomenclatuur: volgens Correa (1969–1985).

1. INTRODUCTION

> "If you ever come upon a grove that is full of ancient trees which have grown to an unusual height, shutting out a view of the sky by a veil of pleated and intertwining branches, then the loftiness of the forest, the seduction of the spot and the thick, unbroken shade of the midst of open space will prove to you the presence of God."
>
> Seneca (ca.50).

Plant ecology and vegetation management

A forest is a living, complex, and dynamic system, driven by the numerous interactions amongst the physical setting, the attributes of its biotic constituents, and the regime of the prevailing ecological impacts. Although a stand of forest trees is a tangible entity, many of these interactions are imperceptible because they operate across a wide array of spatial and temporal scales, ranging from the ancestors to the current members of the population. These "invisible present and place" (Magnuson 1990, Swanson & Sparks 1990) are related to events that happened during a distant past or that occur in the landscape far beyond the site under study. For instance, light radiation beneath the canopy determines microclimatic changes within and around openings over a lapse of seconds and minutes. At the other extreme, forests have changed over thousands or millions of years over entire continents because of climatic change, continental drift, and evolution. Biotic processes such as establishment and species interaction take place at small scales, whereas succession occurs over larger scales.

Forests supply biomaterials (food, medicine, construction material, energy), services (wildlife conservation, environmental quality, habitat diversity and integrity, land productivity, recreation opportunities, aesthetic virtues), and cultural values essential for both geosphere functioning and humanity existence. From ethical and utilitarian standpoints, forests must be managed sustainably, so as to preserve their inherent properties in the long–term. The extent of the life cycle in long–lived organisms such as trees (e.g., 500 years) does not agree with the span of professional careers (e.g., 40 years), economic timber rotations (e.g., 30–80 years), or economic planning cycles (e.g., 1–10 years). This simple fact imposes serious constraints to a rational relationship between society and forests. Forest management evolved from a "custodial" strategy, focusing on avoiding clearly undesirable activities (e.g., overexploitation, fire), towards an agricultural model based on extensive, high–yield sustained production of few necessary commodities (e.g., timber), and finally to a sustainable multiple–use ecosystem management directed to providing a broad array of goods and services (Salwasser 1994). This broad trend reflects the weakness of traditional agricultural–based management approaches, the expanding values that public attaches to forests, the increasing demand for a diversity of resources related to trees and woodlands, and the impressive current rates of forest disappearance and degradation (Oldeman & Sieber–Binnenkamp 1994).

Ecological succession involves the directional, continuous, and non–seasonal pattern of colonisation and extinction of populations in a particular site, leading to eventual changes in species composition, population structures, and vegetational physiognomy (Pickett & White 1985). Vegetation management necessarily implies a controlled series of ecological impacts that result in the re–distribution of resources (light, nutrients, water), and regulators (temperature, moisture), consequently modifying the course of succession (Oldeman 1990). The best approach for maintaining forest integrity and meeting human needs is to use its natural dynamics and the impact regime as a model for management (Oldeman 1990, Attiwill 1994). The study of the basic ecology of forest stands, aimed to understand habitat requirements, regeneration modes, phenology, and architectural dynamics of plants for avoiding, escaping, or resisting impact, is essential to develop an ecologically sound, economically viable, and socially responsible management (Wagner & Zasada 1991). This is also because there is not, nor there will ever be, a simple set of prescriptions for multiple use of complex systems; rather, site–specific prescriptions are always needed. Natural woodlands are particularly valuables in the context of basic and applied scientific research because they constitute a reference point for the comparative analysis of different land management types and environmental monitoring. The ultimate test for scientific understanding of an ecological phenomenon is the ability to use this knowledge to manage ecosystems for conservation. This management approach has been alternatively named "Silvology" (Oldeman 1990), "Holistic forestry" (Mlincek 1991), "New forestry" (Swanson & Franklin 1992), "Forest ecosystem management" (Salwasser 1994), or "Ecological forestry" (Seymour & Hunter 1999).

Current concern regarding the global role and fate of the temperate forests of southern South America is important. Nevertheless, the existing level of knowledge of forest patterns and processes is still inadequate to develop ecologically based management practices. Increased efforts and resources have to be dedicated to better understanding of community structure and functioning, in order to indicate more precisely how sustainable practices should evolve towards a multi–purpose ecosystem management. Deficient knowledge reduces the forester's ability to maintain and enhance values, services, and commodities linked to forested areas. The modification, simplification, and elimination of natural vegetation usually triggers severe deterioration processes in the biota, soil, landscape, and climate. This is particularly relevant in Patagonia, a region characterised by an intrinsic environmental fragility given the seasonal distribution of high rainfall levels, the low temperature, the strong intensity and frequency of winds, and the extensive and deep system of mountain slopes.

The *Austrocedrus–Nothofagus* forests

As one travels from east to west in the Andes' rain shadow of northwestern Patagonia, Argentina, one encounters an abruptly mounting, dissected topography and increasing precipitation. The resulting environmental gradient largely determines an ecological continuum zonation in which different vegetational types occur. At 41°S, the following communities are found: i) steppe, ii) *Austrocedrus chilensis* woodlands and forests, iii) *Austrocedrus chilensis* – *Nothofagus dombeyi* forests (*Austrocedrus chilensis*–dominated), iv) *Nothofagus dombeyi* – *Austrocedrus chilensis* forests (*Nothofagus dombeyi*–dominated), v) *Nothofagus dombeyi* forests, and vi) temperate rainforests. Many studies have been devoted to understanding the ecology of *Austrocedrus chilensis* (D.Don) Florin et Boutelje ("ciprés", "ciprés de la cordillera") (Cupressaceae) and *Nothofagus dombeyi* (Mirb.) Blume ("coihue", "coigüe") (Nothofagaceae). These investigations have mainly focused on either pure forests built by one of these species (Pita 1931, Lebedeff 1942, Frangi 1976, Boninsegna & Holmes 1978, Veblen 1987, Veblen & Lorenz 1988, Dezzotti & Sancholuz 1991, Rovere 1991, Armesto et al. 1992, Veblen et al. 1992b, Gobbi 1994, Villalba & Veblen 1997a,b, Relva & Veblen in press), or on the *Nothofagus dombeyi*–dominated mixed forests (Singer 1971, Eskuche 1973, McQueen 1976, 1977, Veblen & Lorenz 1987). The mixed vegetation type in which *Austrocedrus chilensis* dominates in abundance whereas *Nothofagus dombeyi* appears as a sub–dominant tree, has received little scientific attention. It exhibits the following significant attributes: i) it represents a natural community as the current plants and their ancestors have colonised the site without any trace of human intervention, ii) it constitutes a native community as the plants are indigenous to the site, iii) it represents a virgin community in the sense that many stands have never been exploited commercially, though occasional cutting of a few trees and slight grazing may perhaps have occurred during the recent past, and iv) it comprises a conifer and an angiosperm, two groups of plants that exhibit contrasting evolutionary histories and ecological adaptations.

The retreat of gymnosperms at the evolutionary scale, claimed to be caused by climatic change (Retallack & Dilcher 1981), by the effect of tectonic and volcanic activity (Kershaw & McGlone 1995), or by successional displacement of inferior by superior flowering plants (Regal 1977, Stebbins 1981, Bond 1989, Haig & Westoby 1991), constitutes a major biological theme. In the southern hemisphere, the co–existence of conifer and broadleaved trees in mixed stands constitutes an important scientific subject as well. Unequivocally, the current diversity and geographical distribution of southern conifers is only a minor fraction of that which occurred in the geological past, and consequently the group is often regarded as relictual or "living fossil" (Enright et al. 1995). Compared to woody perennial flowering plants, conifers exhibit a slow rate of individual and population increase (Norton et al. 1987). Many conifers are characterised by discontinuous and restricted age structures indicating failures of regeneration beneath established stands (Enright & Odgen 1995). These features have been formerly interpreted as evidence of their progressive declining, driven by climatic change (Holloway 1954) or by competitive exclusion (Schmithüsen 1960). These ideas were strongly influenced by classic successional theories, based on stable climax communities composed of self–replacing populations. However, these theories did not adequately incorporated impact–driven dynamics (Enright et al. 1995).

The conifer–broadleaved association between *Austrocedrus chilensis* and *Nothofagus dombeyi* is a valuable system for successional studies. Both tree species are very similar in respect to several characteristics. These long–lived, evergreen, mesophanerophytic plants are frequently characterised as light–demanding species, exhibiting a "catastrophic" regeneration mode (Read & Hill 1985, Veblen 1989). They strongly depend after large–surface impacts for colonisation and persistence, showing a limited ability to regenerate beneath the canopy or in small gaps. This is reflected in the ample discontinuity in age structure and large patch size frequently observed in their populations (Veblen 1989). Within the mixed stands, they exclusively show sexual reproduction. A rather clear differentiation in niche requirement occurs with respect to moisture: *Nothofagus dombeyi* and *Austrocedrus chilensis* share the same sites where moisture falls in between the lower limit of tolerance for the former and the upper limit for the latter species.

Objectives

The overall aim of the present research is to reconstruct the history and to analyse the ecological stability of a mixed *Austrocedrus chilensis – Nothofagus dombeyi* stand belonging to the drier mixed type, which developed during secondary succession following a fire, and without subsequent natural or human large–scale impacts. At present, this forest type tends to be dominated in abundance by the drought–tolerant *Austrocedrus chilensis*, while the moisture–demanding *Nothofagus dombeyi* is a sub–dominant tree. Particular objectives of this study are: i) to present a comparative revision of some life histories of conifers and arborescent angiosperms, ii) to outline the main physical, biological, and human–made characteristics of the biome in which this community–type arises, iii) to examine the main evolutionary, biological, and ecological features of *Nothofagus dombeyi* and *Austrocedrus chilensis*, iv) to analyse the performance, age, and spatial structures, growth, regeneration, and dynamics of a forest stand composed of both species, and additionally to estimate the minimal area of this community, and finally vi) to draw a conclusion from the major findings, placing them particularly in the context of current schemes of forest development involving this association. The text is therefore organised in two main parts. The first half of the book (Chapters 2 to 4) summarises the known scientific context, whereas the second half (Chapters 5 and 6) fits the research within this perspective, leading to new insights on the ecology of this mixed forests. Although in terms of geographic distribution the conifer–dominated association may be considered relatively unimportant, a more complete ecological picture of the *Austrocedrus chilensis* and *Nothofagus dombeyi* forests along the environmental gradient in northwestern Patagonia will contribute to fill a significant gap in the knowledge of these subantarctic ecosystems in general, and to complete the understanding indispensable to the manager.

2. ANGIOSPERMS AND GYMNOSPERMS

> "Plants, humans and all other life on this planet are interconnected through ecological systems that have been millions of years in the making, but whatever we humans may think, the chief players are plants, for it is they have made the planet habitable for everything else."
>
> Peter R.Crane (1995).

Evolutionary trends

Gymnosperms arose in the middle Devonian (365 million years before present, Ma) and became the dominant vascular group during the Mesozoic. However, by the end of the late Cretaceous (75 Ma) at least 50% of the plant species were already angiosperms (Lidgard & Crane 1990). At present, flowering plants comprise around 234,000 species compared to only 800 described gymnosperms. This richness exceeds the total number of all other photosynthetic terrestrial plants and algae combined (Givnish 1980, WRI 1986, Thorne 1992). Of the around 4 billion hectares of the world's natural forests, 63% are dominated by broadleaved trees (table 1). The evolutionary and ecological success of flowering plants is reflected by their variety in architecture, size and genotype, local abundance, habitat diversity, and geographical spread. Gymnosperms can be prominent in the landscape as in the northern hemisphere, although they are mostly restricted to high latitudinal and altitudinal environments, characterised by low insolation, cold temperature, and short growing seasons (e.g., the northern boreal and montane forests), or to suboptimal, poor–drained, infertile, or highly acidic soils. They tend to be excluded from extensive forest areas in tropical and subtropical lowland regions with little or no climatic seasonality, and to dominate early successional stages in areas subjected to periodic, large–scale abiotic impacts (Sneath 1967, Woodward 1995).

Evolutionary innovations of angiosperms reproduction were the enclosure of the ovule by carpels protecting the seeds, the further reduction of the male and female gametophytes, and the development of a genuine endosperm that constitutes a food–storage seed tissue. In comparison to gymnosperms, flowering plants exhibit a briefer interval between pollination and seed maturation, a higher seed production, a lower reproductive cost, a shorter life cycle and generation interval, particularly in herbs, a faster sexual maturation, and more mechanisms for vegetative propagation and pollination. Their exclusive vegetative features include a variety of architecture and form (gymnosperms are only woody species with a reduced number of architectural models, showing little or no reiteration (Hallé et al. 1978, but see Edelin 1977)), a great diversity in leaf forms and shapes, an improved leaf conducting and mechanical support system as a heavily vascularized and reticulated venation, and a specialised xylem separated into support and conductive tissues (in gymnosperms tracheids serve both functions, Braun (1963, 1970, *ex* Oldeman 1990)). The diffuse– and ring–porous vessels permits a better conduction than in tracheids because of its larger lumen diameter and size, and the absence of end walls conferring a lower resistance to water flow.

On the base of palaeontological and palaeoecological studies, Taylor & Hickey (1996) describe

Table 1: World forest area in 1973 (10^6ha) (Persson 1974). Mixed broadleaved-dominated forests are mostly included in the broadleaved category. A recent estimate for total forest area is 3,330 10^6ha (Bryant et al. 1997). Percentages of forest land in relation to the area of the region (a), the area covered by the total forest (b), and the area occupied by each forest type (c) are indicated.

Region	Total forest	a	b	Coniferous forest	c	Broadleaved forest	c
North America	630	34	16	466	74	164	26
Central America	65	22	2	21	32	44	68
South America	730	30	18	7	1	723	99
Africa	800	6	19	8	1	792	99
Europe	170	30	4	114	67	56	33
ex-Soviet Union	915	35	23	760	83	155	17
Asia	530	15	13	85	16	445	84
Pacific area	190	10	5	44	23	146	77
Total	4,030	21	100	1,505	37	2,525	63

early angiosperms as small perennial herbs with rapid vegetative growth, short life–span, high allocation of carbohydrates to leaves, clonal reproduction, biotic pollination, carpels, small fruits, and tiny dormant seeds. An improved transport system would have evolved in response to variability in water availability, transpiration, and growth. Their ancestral habitats possibly were nutrient–rich, climatically stable, but frequently disturbed sites under a fluvial regime. Floodplains were earlier invaded by angiosperms evolving secondary growth and beginning to successfully compete against spore–bearing and woody seed plants. The subsequent history of flowering plants comprised an explosive radiation towards different habitats outside the first fluvial setting (Hickey & Doyle 1977). The initial radiation and spread of angiosperms to tropical forests agrees with and extinction of entire orders and families of gymnosperms, as the anemophilic family Cheirolepidiaceae that dominated the Mesozoic communities at low latitudes (Hughes 1977). The divergent hypotheses explaining angiosperm diversification and dominance, and gymnosperm extinction and retreat assume, tacitly or expressly, a causal relationship between these events. Competition in the form of interference and exploitation between these relatively distant groups is presumed to be the main intervening interaction (Hochberg & Lawton 1990). The different life histories are supposed to account for the divergent ecological and biogeographical patterns currently observed within seed plants. The two principal theories explaining the causes for the assumed competitive displacement of gymnosperms by angiosperms differ in the subjacent morphological, functional, and ecological mechanisms. The "reproductive efficiency hypothesis" stresses the value of the reproductive innovation of angiosperms, such as endosperm development and animal pollination and dispersal (Raven 1977, Regal 1977). The "seedling growth hypothesis" emphasises the differences in vegetative habit and primary productivity as the basis for the differential performance between both groups (Stebbins 1981, Bond 1989, Midgley & Bond 1991, Taylor & Hickey 1996) (table 2).

In angiosperms, pollination and dispersal mainly rests upon specific mutualistic interactions with animals, particularly insects, bats, birds, and mammals as pollen and seed vectors. In gymnosperms, wind is the exclusive mechanism for pollination, whereas wind or gravity (for

Table 2: A comparison between the hypotheses explaining the differential performance of spermatophytes.

Concept	Pollination hypothesis (Regal 1977)	Slow seedling hypothesis (Bond 1989)
Primary structural basis for angiosperm advantage	Presence of flower and fruit	Leaf and vascular anatomy, leaf size, architecture
Primary functional effect of angiosperm advantage	Biotic pollination and dispersal	Increased growth and reproduction rates
Predicted gymnosperm distribution	Suboptimal environments	Suboptimal environments
Explanation of gymnosperm distribution	Wind pollination requires dense populations occurring in species-poor communities. In turn, infertile sites cause low diversity	Habitats represent refugees for slow-growing juveniles of conifers
Primary mechanism of gymnosperm displacement by angiosperms	Genetic: heterozygosis is correlated with interspecific competitive ability (wind-pollination syndrome produces more homozigosis than insect pollination syndrome)	Ecological:asymmetric one-sided competition leads to failure in gymnosperm establishment and persistence on productive sites
Absence of gymnosperms in the lowland tropics	Disadvantage of wind-pollinated plants in species-rich, dense communities	Weak competitive ability because of a lower water-use and carbon uptake efficiency
Dominance of gymnosperms in non-marginal environments	Not explained	Not explained

winged seeds enclosed in wooden cones) and animals (for fleshy structures as arils bearing wingless seeds) are involved in dispersal (Givnish 1980). In flowering plants, the pollination system would obtain selective advantages from increases in i) the gene dispersal efficiency, because it is specific and cost–effective allowing the maintenance of long distant gene flows among widely spaced individuals, ii) the colonisation rate to new and safer sites by outcrossed offspring after long–distant seed dispersal, iii) the mate choice rate, because it permits careful screening of partners, and vi) the speciation rate as a result of the co–evolution with pollinators and dispersers (Raven 1977, Regal 1977, Burger 1981, Doyle & Donoghue 1986). Additionally, the carpels represent a potential isolation mechanism providing an additional force driving speciation. Gymnosperms were able to persist and dominate in extensive habitats where wind pollination is as effective as animal pollination. In environments reducing wind speed, such as the lowland tropical forests, anemophilic gymnosperms are especially inefficient. On the contrary, wind pollination may be of no particular disadvantage where individuals are closely spaced, and features other than pollination mainly if not totally decide competitive superiority.

Bond (1989) argues that the prosperity of angiosperms benefits from vegetative and reproductive strategies rather than from mate access and selection. On the one hand, the attributes associated with the herbaceous habit, such as rapid growth, short reproductive cycle, and low maintenance cost permit angiosperms to attain higher establishment rates in a larger array of habitats like ephemeral and early seral ones. On the other hand, the high productivity of some conifers results from the accumulation of several cohorts of leaves over long periods, rather than from the comparatively low leaf photosynthetic rate, a strategy reinforced by the great period of activity of functional tracheids, up to ten years (Braun 1963, 1970, *ex* Oldeman 1990). Gymnosperm seedlings indeed exhibit a single cohort of leaves and therefore represent a slow–growing phase, until sufficient growth rings are formed in the wood. The consequence of this phylogenetic constraint is that the regenerative stages tend to be restricted to sites or to successional stages characterised by low competition. The weedy seedlings permits many angiosperms a rapid colonisation and persistence in sites where conditions and resources stimulate rapid growth. Because of competition with such plants, gymnosperms would fail in establishing themselves, experience further decrease in growth, and suffer increased size–dependent mortality and vulnerability to pests, pathogens, and other stresses.

The reproductive hypothesis for the rise to dominance in angiosperms based on biotic gene dispersal, mate choice, and speciation rate, favoured by the concomitant evolution of pollinators and dispersers, was criticised. The generalisation that wind pollination is comparatively less efficient than other mechanisms, because of lower pollen mobility, is questioned. Viable seeds of conifers located in dense forests were found at a considerable distance from the nearest reproductive parent (Bond 1989). The occurrence of fossil (e.g., Benettitales) and extant (e.g., cycads) insect–pollinated, pre–angiosperms species would indicate that zoophily has long preceded the appearance of the flower (Midgley & Bond 1991). The argument that biotic gene dispersal boosts the speciation rate is in conflict with the presence of very diverse families of wind–pollinated monocotyledonous and dicotyledonous plants, such as members of the Gramineae, Cyperaceae, Fagaceae, and Nothofagaceae (Midgley & Bond 1991). It is questionable whether or not this strategy represents an evolutionary force for angiosperm success, as many non–living and living gymnosperms depend on animals for dispersion. For instance, Givnish (1980) identified 357 wind–dispersed (monoecious with cones) and 447 animal–dispersed (dioecious with fleshy fruits) gymnosperms. The term “fruit” is used here in its ecological and functional sense, although gymnosperms have no genuine fruits. Furthermore, early angiosperms were abiotically dispersed, and fleshy fruits and appropriate frugivorous birds became common long after angiosperm radiation (Tiffney 1984). The timing of early insect – angiosperm co–radiation, and the cause – effect relations remain obscure. For instance, Labandeira & Seproski (1993) proposed that the origin of many modern families of flower–visiting insects originated in the Jurassic. Therefore, the early radiation of angiosperms during the Cretaceous would have had no effect on insect diversity. Contrarily, Grimaldi (1999) argues that major anthophilic insects as bees, pollen wasp, flies, and Lepidoptera took place in the lower Cretaceous, and that the pattern of their diversification is consistent with the origin of entomophilous syndromes in early flowers. None of the two models provide an explanation for the existence of extensive conifer–dominated forests in the mild wet oceanic climates, such as the Pacific Northwestern Forests of North America.

Longevity and growth

A distinction in life history between gymnosperms and woody angiosperms comprises longevity. Loehle (1988) compared 145 tree species from the northern hemisphere, reporting a mean longevity of 346 years for gymnosperms (average maximum longevity 596 years), and 139 years for angiosperms (219 years) (table 3). For southern gymnosperms, Enright & Odgen (1995) estimated a mean typical longevity of 486 years (range: *Actinostrobus arenarius* (Cupressaceae) 20 years, *Fitzroya cupressoides* (Cupressaceae) 1,200 years) (N= 28 species), and a mean maximum longevity of 771 years (*Actinostrobus arenarum* 100 years, *Fitzroya cupressoides* 3,621years) (N= 43). In New Zealand, Odgen & Stewart (1995) examined longevity of trees in mixed conifer–broadleaved stands, finding the same trend: a range of typical longevity between 370 and 524 years for broadleaved trees, and between 560 and 981 years for conifers. Longevity of southern angiosperms woody perennials appears to be similar to that of northern angiosperms (Enright & Odgen 1995). These results together with those reported by Loehle (1988), indicate that gymnosperms, regardless the geographic distribution, are intrinsically longer–lived than angiosperms. However, the greater capacity for reiteration following trunk damage or in crown expansion observed in several members of the latter group, as a result of rather weak architectural conformity, makes them virtually immortal (Hallé et al. 1978).

Plant growth is a physiological process that depends on the interaction of several environmental resources (light, temperature, carbon dioxide, water supply, air humidity, nutrients), and conditions (e.g., salinity, pollutants, pathogens) (Kozlowski & Pallardy 1997b). Growth integrates

Table 3: Compared mean values of different life history characteristics between gymnosperms and woody angiosperms from the northern hemisphere. The range (R) of the variables and the sample size (N) is indicated. Primary data compiled by Loehle (1988).

Characteristics	Gymnosperm			Angiosperm		
	Mean	R	N	Mean	R	N
Wood heat content (HC, J cm^{-3}) [(a)]	7.9	6.4–11.0	21	9.8	6.4–13.2	25
First reproduction (yr) [(b)]	36	12–100	47	29	2–75	58
Typical longevity (yr) [(c)]	346	60–2,000	58	139	15–350	87
Maximum longevity (yr) [(d)]	596	150–3,500	55	219	15–600	71
Average growth rate class [(e)]	2.8	1–4	59	3.2	2–5	88

Gymnosperms: *Abies* (8 species), *Chamaecyparis* (3), *Cupressus* (1), *Juniperus* (5), *Larix* (2), *Libocedrus* (1), *Picea* (6), *Pinus* (23), *Pseudotsuga* (1), *Sequoia* (2), *Taxodium* (1), *Taxus* (1), *Thuja* (2), *Tsuga* (3). Angiosperms: *Acer* (5), *Aesculus* (2), *Alnus* (1), *Arbutus* (1), *Betula* (4), *Calluna* (1), *Carya* (6), *Castanea* (1), *Castanopsis* (1), *Catalpa* (1), *Celtis* (2), *Coffea* (1), *Cornus* (2), *Diospyros* (1), *Dryas* (2), *Erica* (2), *Fagus* (1), *Fraxinus* (5), *Gleditsia* (1), *Ilex* (1), *Juglans* (2), *Liquidambar* (1), *Liriodendron* (1), *Lithocarpus* (1), *Maclura* (1), *Magnolia* (2), *Morus* (1), *Nyssa* (2), *Ostrya* (1), *Platanus* (1), *Populus* (6), *Prunus* (1), *Purshua* (1), *Quercus* (23), *Rhamnus* (1), *Robinia* (1), *Salix* (1), *Sassafras* (1), *Thymus* (1), *Tilia* (2), *Ulmus* (3), *Umbellularia* (1). (a) A measure of both physical and chemical defence costs. HC= wood density (g cm^{-3}) * wood caloric content (J g^{-1}). (b) Age at which trees produce a good crop of seeds. (c) Age of the older trees in an old–growth stand. (d) Upper known maximum above which very few trees are found. (e) Growth rate classes vary between 1 (very low growth) to 5 (very fast growth).

the effects of several other physiological and ecological mechanisms (e.g., photosynthesis, respiration, allocation, and competition). Tree growth habit involves a maximisation of the life–cycle length and a priority to height growth, via accumulation of functional, living or death, woody biomass in the stem in a very great proportion in relation to total biomass. This trend conducting to perennial, large–sized, long–lived plants is particularly extreme in gymnosperms, a group that would include the biggest and oldest organisms on earth (e.g., *Sequoiadendron giganteum* (Taxodiaceae) 2,030 Mg, *Pseudotsuga menziesii* (Pinaceae) 126m, *Pinus aristata* (Pinaceae) 4,900 years). The evolutionary and ecological success of plants is strongly dependent on body size. A rapid growth in size should therefore increase the chances of an individual to escape early size–dependent inter– and intraspecific mortality, to reach reproductive size earlier, and to reproduce at a greater rate sooner (McGraw & Garbutt 1990, Tilman 1997). However, the relationship between individual plant growth and fitness is not simple. There are numerous and unavoidable trade–offs between allocation to high productivity and allocation to survival (e.g., defence against herbivores and frost) and reproduction (e.g., production of flowers, nectar, and seeds) (Crawley 1997a). For instance, the morphological and biochemical characteristics of a leaf positively correlated to maximum photosynthesis are negatively correlated to defence, desiccation, and physical integrity (Reich et al. 1992, Crawley 1997a). Broad comparative studies of growth rates among groups of plants provide a deeper understanding on the adaptive significance of growth variation and the potential trade–off with other characters. Syndromes of plant growth are the basis for the theories of plant life history strategies (e.g., Grime 1979, Tilman 1997).

Are there inherent differences in adult growth rate comparing gymnosperms and woody and herbaceous angiosperms, which in turn can be tested as an explanation of the divergent ecological roles played by both groups? Firstly, growth is certainly a property of the individual plant, and therefore an individual–based approach is essential from an ecological and evolutionary perspective. A comparative analysis primarily includes the interplay amongst the net photosynthetic rate of leaves (NAR, on the basis of area or weight), the amount of photosynthetic surface (leaf area index, LAI) and its duration (leaf life–span, LLS), the whole–plant respiration (R), the length of the growing season (T), and the pattern of photosynthate allocation between leaves and non–photosynthetic tissues (LWR, leaf weight ratio= leaf weight / plant weight) (Kozlowski & Pallardy 1997b). A fast–growing leaf does not necessarily imply a fast growing plant, and a fast– growing plant at a certain development stage does not necessarily imply a fast–growing species. Secondly, comparative data are difficult to find because of the huge sources of variation involved in such measurements related to physical conditions, technical devices, growth parameters, period of measurements, pre–treatments, and plant characteristics and provenance. For instance, short–term measurements of CO_2 uptake often have been made in controlled environments. However, such an environment may not be favourable to all species studied. Broadleaved species show photosynthesis equally efficient at low as well as at high light intensities, whereas several gymnosperms are much more efficient at a high intensity regime. Tranquilini (1962) found that the rate of photosynthesis of *Larix decidua* (Pinaceae) was twice that of *Pinus cembra* on a leaf weight basis, but their rates were similar when expressed per leaf area unit denoting that the latter had a heavier leaf.

In large woody plants, respiration cost associated to the progressive accumulation of non–photosynthetic, supportive tissue is responsible for the decrease in individual assimilation rate compared to herbs. Nevertheless, is there a differential assimilation capacity between leaves of woody and non–woody plants? The idea that woody plants tend to exhibit an inherently lower NAR than those of herbaceous plants, and particularly of agricultural crops, is present in literature (e.g., Jarvis & Jarvis 1964, Larcher 1980). Differences were attributed to some factors linked to wood formation, incompatible with high growth rates. However, Nelson (1984) compiled information on NAR and concluded that a variety of woody plants, including deciduous and evergreen angiosperm trees, angiosperm shrubs, and conifers are well within the range of the agricultural and herbaceous plants (table 4). Lower NAR erroneously attributed to woody plants was due to several confounding factors: measurement made in suboptimal environments, inadequate experimental control, utilisation of thin shade leaves with low NAR per unit area (Nelson 1984).

Aboveground net primary productivity (NPP, at stand level basis) of temperate forests varies from 1 to 40 Mg $ha^{-1}yr^{-1}$, approximately (Jarvis & Leverenz 1983). Several sources of variation are encompassed within this interval. They are included the time within the development cycle the growth is measured, and the period of time over which growth is averaged (e.g., mean annual increment is frequently smaller than current annual increment (Smith et al. 1997)). Comparative studies on the aboveground NPP in broadleaved and conifers stands were seldom carried out under such similar conditions, as those found in close stands at comparable development stages. Nevertheless, those infrequent analyses show that the productive capacity of northern hemisphere conifers equals or exceeds that of broadleaved deciduous trees (Schultze et al. 1977, Alban et al. 1978, Satoo & Madgwick 1982) (table 5). Also, they reflect the complex interplay of single growth–controlling parameters as NAR, LAI, and T. Jarvis & Leverenz (1983) compiled data on maximum total NPP of temperate stands, concluding that there is no evidence of the claimed generalisation on the growth superiority of angiosperms over gymnosperms during the adult stage (table 6). In conifer–dominated stands, the shape and mean value of the normal frequency distribution of NPP is equivalent to that in evergreen broadleaved–dominated stands, indicating also that both forest types exhibit a similar productivity pattern (Barnes et al. 1988).

Table 4: Maximum mean values of net assimilation rate (NAR) of adult trees growing under an optimal condition. Primary data compiled by Nelson (1984).

Species	NAR ($\mu g\ CO_2 g^{-1} s^{-1}$)
Agricultural plants	8.3 - 16.7
Angiosperms	
Alnus rubra	11.1
Populus balsamifera x *P.tristis*	11.1
Populus nigra x *P.deltoides*	12.3
Salix (several species)	13.5 - 17.2
Gymnosperms	
Pinus rigida	14.5
Pinus sylvestris	9.7 - 10.5
Pinus taeda	11.1
Pseudotsuga menziesii	9.7

Table 5: Total net primary productivity (NPP) of conifer (underlined) and angiosperm species growing in adjacent sites.

Region	Species	Age (yr)	NPP (Mg ha^{-1}yr^{-1})
Germany (Schultze et al. 1977)	*Picea abies*	89	8.4
	Fagus sylvatica	120	4.2
U.S.A. (Alban et al. 1978)	*Picea glauca*	40	3.5
	Pinus banksiana	40	3.5
	Pinus resinosa	40	5.0
	Populus spp.	40	4.2
Japan (Satoo & Madgwick 1982)	*Abies sachalinensis*	26	13.0
	Larix leptolepis	21	16.5
	Picea abies	46	7.3 - 12.4
	Betula maximowiziana	47	4.2 - 6.2
	Populus davidiana	40	8.7

In the temperate zone, seasonal changes in photosynthetic capacity associated to climatic conditions occur more gradually in gymnosperms than in deciduous angiosperms, due to the great stability of

Table 6: Maximum total net primary productivity (NPP) of some temperate stands. Primary data compiled by Jarvis & Leverenz (1983).

Species	NPP (Mg ha^{-1}yr^{-1})
Gymnosperm	
Abies grandis	22
Abies sachalinensis	29
Cryptomeria japonica	53
Picea abies	22
Picea sitchensis	24
Pinus nigra	25
Pinus radiata	34
Pseudotsuga menziesii	28
Sequoia sempervirens	23
Thuja plicata	20
Tsuga heterophylla	30
Angiosperm	
Eucalyptus globulus	40
Eucalyptus grandis	41
Eucalyptus nitens	22
Populus balsamifera x tristis	33
Populus deltoides x nigra	23
Salix matsudana x alba	34
Salix purpurea	36

sapstream in many living rings (Oldeman 1990). In deciduous angiosperms, the rate of photosynthesis typically accelerates rapidly in spring as trees refoliate, remains high during summer, and declines abruptly in late summer or early autumn with leaf senescence (Kozlowski & Pallardy 1997b). The usual evergreen habit of conifers tends to compensate for any difference in growth rate because photosynthesis can continue for extended periods (Ovington 1956, Pollard & Wareing 1968, Schultze et al. 1977, Linder & Troeng 1980, Lassoie et al. 1985). For instance, though the deciduous *Fagus sylvatica* (Fagaceae) exhibited a NAR two to four times higher than that of the evergreen *Picea abies* (Pinaceae), the latter yielded a NPP near two times higher than that of the former as a result of their more numerous cohorts of leaves (larger LAI) and a longer growing season (T= 260 days against 176 days) (Schultze et al. 1977) (table 6).

McGregor & Kramer (1963) associated the contrasting NPP of two pine species to the fact that the fast growing *Pinus taeda* made three flushes of shoot growth adding new needles until late summer, whereas the slow growing *Pinus strobus* made only one. In northwestern North America, the wide distribution and dominance of gymnosperms has been related to their higher nutrient use efficiency (dry matter production / unit of nutrient), and to their high potential for NAR outside the growing season (e.g., *Pseudotsuga menziesii* exhibits 50–70% of annual photosynthesis outside the summer months, Lassoie et al. 1985). Moreover, in frost–free winter days gymnosperms can intercept all incident light while leafless angiosperms do not capture any light (Hallé et al. 1978, Oldeman 1990). Hence, in dormant periods within seasonal climates, evergreen angiosperms often exhibit a positive carbon balance whereas deciduous angiosperms lose biomass through respiration. Consequently, an evergreen tree with a slightly lower rate of photosynthesis during the growing season may accumulate more biomass over a year because of the extended period of photosynthetic activity (Lassoie et al. 1985). During winter under Mediterranean–type climates, the photosynthetic capacity of evergreen trees is reduced only slightly while deciduous trees recurrently show a negative carbon balance (Kozlowski & Pallardy 1997b). However, in regions with extreme winters the photosynthetic rate of conifers is negligible during periods of severe frost (Kozlowski & Pallardy 1997b). Retention of foliage late into the autumn is an important factor contributing to the rapid growth of some broadleaved trees, as shown for instance by Nelson et al.(1982), Neave et al.(1989), and Amthor et al.(1990). Autumnal leaf retention is particularly marked in juvenile trees (Oldeman pers.com.), which then show a similar winter strategy as gymnosperms.

Juvenile growth

Although gymnosperms exhibit an intrinsic growth capacity equivalent to angiosperms during the adult stage, there is compelling evidence indicating that this statement is not correct when comparison are made between juveniles. Inherent growth differences are observed both in absolute terms and when comparisons are made between angiosperms and gymnosperms with overlapping geographical distribution. Under any given set of conditions, contrasts in relative annual rate of dry matter production per unit of total weight (RGR) can be attributed to divergences in the rate of carbon fixation per unit of leaf surface (NAR per unit area) and/or the proportion of productive material within the plant (LAR, leaf area ratio= leaf area / plant weight). The components of the relative growth RGR= NAR * LAR permit to determine whether or not a plant gains its growth superiority from a greater photosynthetic performance and/or a greater relative allocation of carbohydrates to photosynthetic surface (Kozlowski & Pallardy 1997b). This growth analysis approach has been used frequently in juvenile trees because of the easy experimental manipulation of small plants.

Lower production in gymnosperm seedlings is caused either by a lower photosynthetic rates (NAR per unit of foliage area or weight), a lower absolute (LAI) or relative foliage biomass (LWR, LAR), or a combination of all these factors. Kozlowski (1949, *ex* Kozlowski & Pallardy 1997b) found that under shaded and unshaded conditions, 3–year old seedlings of *Quercus lyrata* (Fagaceae) reached a significantly larger size and weight than *Pinus taeda* seedlings (table 7). Ovington (1960) reported that in plantations, during the first years of development hardwoods grew faster than pines as a result of their higher allocation to leaves (LAR and LWR). However, older plantations of *Pinus* had higher production of dry matter than that of *Betula* (Betulaceae), *Acer* (Aceraceae), and *Populus* (Salicaceae). Logan (1966, *ex* Kozlowski & Pallardy 1997b) examined growth responses to different light intensities by seedlings of two species of *Betula* and *Acer*, of *Larix decidua*, and of three species of *Pinus*. Regardless of luminosity, the absolute aboveground growth rate of broadleaved seedlings was substantially superior to that of conifers (table 8). Juveniles of the deciduous *Acer pseudoplatanus*, *Betula verrucosa*, and *Populus tremula* attained a higher relative growth rate (RGR= 0.072–0.075g g^{-1}day^{-1}) than those of *Picea abies*, *Pinus radiata*, and *Pinus sylvestris* (RGR= 0.005–0.048g g^{-1}day^{-1}), according to Jarvis & Jarvis (1964) and Pollard & Wareing (1968). This was mainly a result of higher allocation of carbon to productive tissues measured as LAR (table 9). Under a very shaded environment, seedlings of the light–demanding *Alnus rubra* (Betulaceae) outgrew those of *Picea sitchensis* and *Tsuga heterophylla* (Pinaceae) as a consequence of greater leaves biomass and surface, although no differences in proportional biomass allocated to photosynthetic tissues between plant groups were recorded (Ruth 1967, *ex* Krueger & Ruth 1969). *Liquidambar styraciflua* (Hamamelidaceae) seedlings exhibited a higher diameter, height, and total weight than *Pinus taeda* seedlings under different irradiance regimes, ascribed primarily to higher leaf photosynthetic capacity NAR (Tolley & Strain 1984, Sionit et al. 1985) (table 10). Krueger & Ruth (1969) compared the physical and growth characteristics of 2–year old seedlings of *Alnus rubra*, *Pseudotsuga menziesii*, *Picea sitchensis*, and *Tsuga heterophylla* (Pinaceae). Under two light regimes, the broadleaved species achieved significantly higher total and leaf dry weight, primarily linked to higher partitioning of photosynthate to leaves and leaf photosynthetic capacity (table 11). In

Table 7: Physical and growth properties of 3-year old angiosperm and gymnosperm (underlined) seedlings, growing under different light regimes in a simulated natural condition. H= total height, DWs= stem dry weight, DWr= root dry weight, and GR= absolute growth rate (Kozlowski 1949, ex Kozlowski & Pallardy 1997b).

Variable	*Quercus lyrata*		*Pinus taeda*	
	shaded	unshaded	shaded	unshaded
H(cm)	66	59	35	42
DWs (g)	20.1	21.1	7.2	20.1
DWR (g)	38.7	44.1	6.1	25.2
GR (g yr^{-1})	19.6	21.7	13.3	15.1

Table 8: Physical and growth properties of 5-year old angiosperm and gymnosperm seedlings, growing under two light regimes. GR= absolute above-ground growth rate, DWL= leaf dry weight, DWs= stem dry weight, H= total height (Logan 1965, 1966, ex Kozlowski & Pallardy 1997b).

Species	H (cm)		DWs (g)		DWL (g)		GR (g yr^{-1})	
	25%	100%	25%	100%	25%	100%	25%	100%
Angiosperms								
Acer saccharinum	121.9	76.2	44.2	50.7	27.5	50.4	14.3	20.2
A. saccharum	144.8	139.7	76.6	235.0	43.3	154.6	23.4	77.9
Betula papyrifera	203.2	152.4	156.7	243.4	54.9	96.6	42.3	67.9
B. alleghaniensis	195.6	149.9	154.8	236.2	51.1	95.0	41.2	66.2
Gymnosperms								
Larix decidua	111.8	170.2	10.2	40.7	-	-	2.0	8.1
Pinus banksiana	73.7	111.8	16.2	52.7	-	-	3.2	10.5
P. resinosa	30.5	40.6	4.4	23.5	10.1	38.5	2.9	12.4
P. strobus	38.1	55.9	5.4	22.7	13.6	31.3	3.8	10.8

gymnosperms, lower growth has also been attributed to mutual shading giving the aggregation of needles in fascicles, consequently light intensity for saturation should be many times higher than in angiosperms (Kramer & Decker 1944, Kramer & Clark 1947). The fact that the RGR of conifer seedlings and saplings is relatively low is consistent with the longer life–span of their leaves (LLS) and lower NAR based on weight (Grime & Hunt 1975, Reich et al. 1992). LLS is highly correlated with metabolism, growth, and carbon allocation (Reich et al. 1995). Short LLS is found under conditions favourable to greater carbon gain, for instance in fertile sites and sunny environments. The same trend is also observed in sites where unsuitable growth conditions arise regularly, in which plants maximise carbon assimilation outside these periods. Variation among species in maximum seedlings RGR is well correlated with LLS: species with long LLS tend to have thick leaves and low

Table 9: A comparison of the leaf area ratio (LAR, leaf area / total dry weight), net assimilation rate (NAR), and maximum relative growth rate in dry weight (RGR) of 20 to 61-day old broadleaved and coniferous seedlings. An herbaceous plant is shown for comparison (Jarvis & Jarvis 1964, Pollard & Wareing 1968).

Species	LAR (cm^2 g^{-1})	NAR (g m^{-2} day^{-1})	RGR (g g^{-1} day^{-1})
Angiosperm herb			
Helianthus annuus	171	8.19	0.140
Angiosperm trees			
Betula verrucosa	166	4.41	0.073
Acer pseudoplatanus	138	5.50	0.075
Populus tremula	227	3.17	0.072
Gymnosperm trees			
Picea abies	18	2.70	0.005
Pinus radiata	88	5.40	0.048
Pinus sylvestris	36	3.24	0.012

Table 10: Physical and growth properties of angiosperm and gymnosperm (underlined) seedlings, growing under a simulated favourable condition. DWL= leaf dry weight, DWR= root dry weight, DWS= stem dry weight, DWT= total dry weight, GR= absolute growth rate, and NAR= net assimilation rate (Sionit et al. 1985)[(a)].

Variable	*Liquidambar styraciflua*	*Pinus taeda*
DWS (g)	2.1	0.4
DWL (g)	1.5	1.4
DWR (g)	6.3	2.1
DWT (g)	9.9	3.9
LWR (g g^{-1})	0.2	0.4
NAR (μmol $CO_2 m^{-2} s^{-1}$)	11.0	3.5
GR(g $week^{-1}$)	0.3	0.1

(a) The purpose of the experiment was to analyse production responses of co-occurring species under long-term enhancement in atmospheric CO_2 content. Here, only assimilation rates under normal CO_2 concentration (350μL L^{-1}, control treatment) are indicated. NAR was measured in 4-week old seedlings, the rest of the variables in 32-week old seedlings.

SLA (specific leaf area= leaf area / leaf weight), low N content, low photosynthetic rates, and low leaf area per whole plant mass (LAR); in combination, these traits limit maximum RGR (Poorter et al. 1990, Reich et al. 1992).

Table 11: Physical and growth characteristics in angiosperm and gymnosperm (underlined) 2-year old seedlings, growing in two light regimes under controlled conditions in laboratory. S= Shaded, L= Unshaded. DWT= total dry weight, DWL= leaf dry weight, LA= leaf area, SLA= specific leaf area (= LA/DWL), LWR= leaf weight ratio (= DWL/DWT), LAR= leaf area ratio (= LA/DWT), DR= dark respiration, NAR= net assimilation rate, and RGR= relative growth rate (= NAR * LAR) (Krueger & Ruth 1964).

Variable	*Alnus rubra*		*Pseudotsuga menziesii*		*Picea sitchensis*		*Tsuga heterophylla*	
	S	L	S	L	S	L	S	L
DWT (g)	0.7	1.8	0.2	0.5	0.1	0.1	≈0.1	0.1
DWL (g)	0.3	0.7	0.1	0.2	≈0.1	0.1	≈0.1	≈0.1
LA (cm^2)	83.0	117.0	11.0	21.0	2.7	4.2	2.1	2.6
SLA ($cm^2 mg^{-1}$)	0.3	0.2	0.2	0.1	0.1	0.1	0.1	0.1
LWR (g g^{-1})	0.5	0.4	0.5	0.4	0.5	0.5	0.4	0.4
LAR ($cm^2 g^{-1}$)	127.7	66.1	55.0	45.7	54.0	35.0	52.5	52.0
DR ($mgCO_2 g^{-1} h^{-1}$)	2.6	2.4	1.6	1.5	1.5	1.8	1.5	1.5
NAR ($mgCO_2 dm^{-2} h^{-1}$)	15.0	17.6	14.1	14.9	11.8	14.3	9.6	11.2
RGR ($mgCO_2 g^{-1} h^{-1}$)	19.1	11.6	7.8	6.8	5.4	5.0	5.1	5.8

In young gymnosperms, an inferior growth capacity is expected as a prelude to increased mortality by competition. This is particularly important in sites with adequate supply of resources and suitable conditions, or with frequent abiotic and biotic impacts. In these locations, a vigorous invasion by angiosperm trees, shrubs, and herbs occurs. Caldwell et al.(1995) found that in seedlings of *Pinus resinosa* growing together with grasses, shoot length, root collar diameter, and needle length was reduced by 40, 54, and 20%, respectively, in comparison with the dimension of seedlings growing in monocultures. However, this intrinsic low growth capacity is not a constant characteristic over the whole life–span (Oldeman & van Dijk 1991). If immature gymnosperm survive beyond the initial stage of establishment, as in low–resource or suboptimal–condition sites, they tend to move to a growing stage closer to angiosperms (tables 4, 5, 6). The reversal in conifer productivity from seedling to mature tree is explained by the accumulation of a large leaf mass. A large leaf area index (LAI) and total foliage biomass (LWR) develops as a result of the accumulation and maintenance of long–lived leaves (LLS) (Reich et al. 1992, Gower et al. 1993). Yet, due to differences in allocation and allometry trees with a shorter leaf life–spans may still be taller than those with a longer leaf–span foliage. A larger leaf accumulation takes many years to develop. For instance, maximum LAI is attained within 5 years in broadleaved deciduous forests, while in *Picea sitchensis* and *Pinus sylvestris* stands it takes between 16 to 40 years (Jarvis & Leverenz 1983, Bond 1989). In closed–canopy stands, total foliage mass per unit of land increases sharply with increasing leaf life–span among species, measured both for different sites and within a site (Gower et al. 1993, Reich et al. 1995). Later, as leaf area increases, conifer productivity gradually exceeds that of deciduous angiosperms.

3. THE BIOME

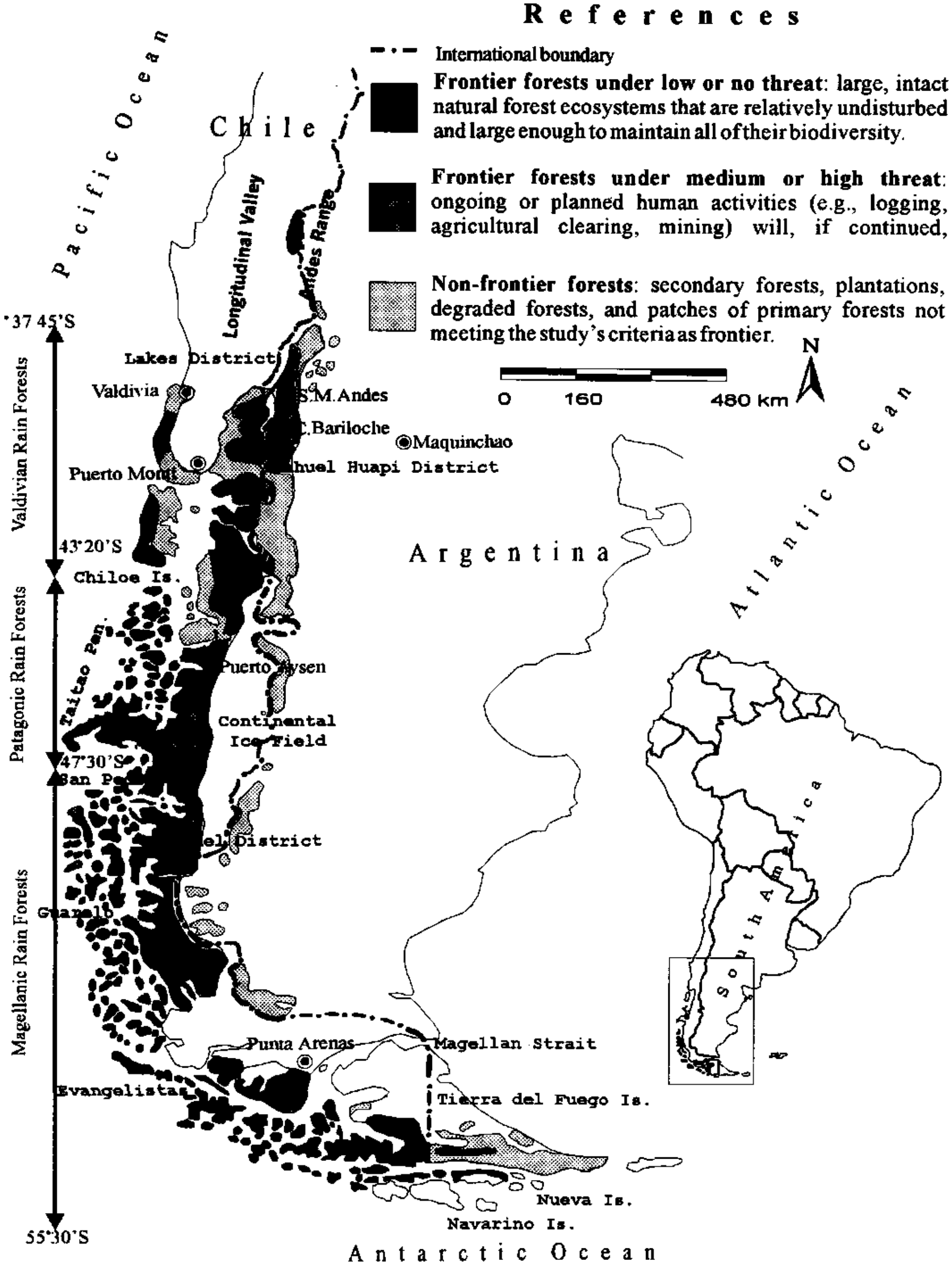
> "On every side were lying irregular masses of rock and up-torn trees; other trees, though still erect, were decayed to the heart and ready to fall. The entangled mass of the thriving and the fallen reminded me of the forests within the tropics; yet there was a difference, for in these still solitudes, Death, instead of Life, seemed the predominant spirit."
>
> Charles Darwin (1839).

Climate

The Subantarctic Forest biome comprises a continuous narrow fringe of woodlands dominated by evergreen and deciduous trees, located at both sides of the southern Andes from ca. 38°S to the end of the continent at ca. 55°S. (figure 1). The western part of southernmost South America is characterised by a cold–temperate, non–seasonal, humid, windy climate, with a pronounced transition to more seasonal and xeric conditions towards the north and the east (Almeyda & Sáez 1958). The climate is mainly determined by the presence of i) the subtropical high pressure cell over the south–eastern Pacific ocean (the Subtropical Anticyclone of the SE Pacific) and the circumpolar belt of a migratory low pressure cell, which in combination determine the general air circulation pattern, ii) the massive Andes range, which mainly defines a strong west–east moisture gradient, iii) the Pacific ocean, which contributes to a remarkable temperature homogeneity and extreme moderation throughout the year, and iv) Antarctica, the proximity of which to the southernmost part of the continent induces a much colder climate than that of the northern hemisphere at the same latitude (Aceituno et al. 1993).

The Pacific anticyclone is located between 31° and 42°S, but changes in intensity and latitudinal position over the year. In austral summer, it is weaker and lies near the southern end of this fringe, and in austral winter, it is more intense and lies in the northern end. In agreement with the position of the high and low pressure cells, strong westerly Pacific moist winds blow predominantly following a south–eastward direction, giving rise to heavy rains and cloudiness. Nevertheless, thunderstorms and other manifestations of strong convection are practically unknown in the region. In some places along the Pacific coast near the centre of this southern zone, the average annual wind speed is 12m s^{-1} with every month recording a maximum exceeding 30m s^{-1}. Wind direction is remarkably constant, with a westerly component present at least 75% of the time. The moist air from the west is forced to rise abruptly near the ocean edge and is turned southward as it approaches the coastline. This process accounts for the extremely high rainfall recorded over the Chilean islands located between 48°–52°S For instance, at Guarelo island (50°21'S–75°21'W, 15m) a mean annual rainfall of 7,330mm with more than 300 rainy days has been recorded (Oficina Meteorológica de Chile 1965, *ex* Miller 1976).

The annual temperature amplitude at sea level (mean temperature of warmest month minus mean temperature of coolest month) increases southward from 7.9 to 8.8°C (Arroyo et al. 1993). The daily temperature amplitude is about 6°C in the extreme north and 4°C in the extreme south



- International boundary
- **Frontier forests under low or no threat**: large, intact natural forest ecosystems that are relatively undisturbed and large enough to maintain all of their biodiversity.
- **Frontier forests under medium or high threat**: ongoing or planned human activities (e.g., logging, agricultural clearing, mining) will, if continued,
- **Non-frontier forests**: secondary forests, plantations, degraded forests, and patches of primary forests not meeting the study's criteria as frontier.

Figure 1: Geographic distribution of the vegetational districts in the temperate rainforests of South America (Veblen et al.1983), and their conservation status (Bryant et al.1997).

(Miller 1976). This relatively high thermal equability observed along space all year round is a consequence of a low land / ocean ratio, a quotient that decreases with latitude. This climatic pattern is reflected by the meteorological data from the following stations (ordered by latitude): Valdivia (39°48'S–73°14'W, 6m), annual rainfall 2,676mm, mean annual temperature 11.6°C; Puerto Montt (41°28'S–72°57'W, 13m), 1,983mm, 11.1°C; San Pedro (47°43'S–74°55'W, 22m), 4,485mm, 8.2°C; Evangelistas (52°24'S–75°06'W, 55m), 2,570mm, 8.2°C; Isla Nueva (55°10'S–66°36'W, 14m), 738mm, 5.6°C. The subtropical anticyclone inhibits the northward movement of the moist westerlies increasing the vertical stability of the air masses, and therefore the climate of a Mediterranean type and finally a desert type arises (e.g., Valparaíso, 33°01'S–71°38'W, 41m, 490mm, 14.3°C). Towards the extreme south, annual precipitation decreases, although moisture remains high because temperature decreases as well (e.g., Punta Arenas, 53°09'S–70°56'W, 2m, 492mm, 6.7°C).

Within the biome, the strong west–east climatic variation associated with increasing aridity, coldness, and continentality is explained by the Andes' "rain shadow" effect on the strong westerly humid airflow. South of 34°S, the Andes becomes a single, fairly narrow range, the altitude of which begins to diminish steadily from about 5,000m at the northern end, to around 2,000m at the southern end near the Straits of Magellan. The maritime air is forced upwards on reaching the foothills, becomes colder and compressed vertically, causing an orographic rainfall. Contrarily, the airflow on the lee descends and expands producing a trough of low pressure, so there is a persistent dry wind over much of the year. This produces a semiarid steppe within the Patagonian plain. At 42°S in the eastern foothill of the Andes, the annual precipitation exceeds 4,000mm, decreasing to around 600mm within 70km. This pattern is reflected in the following stations (ordered by longitude): Puerto Blest (41°50'S–71°50'W, 630m), 4,000mm, 9°C; San Martín de los Andes (40°08'S–71°21'W, 640m), 1,379mm, 8.8°C; San Carlos de Bariloche (41°09'S–71°18'W, 760m), 1,096mm, 8.4°C; Maquinchao (41°15'S–68°44'W, 400m), 178mm, 9.3°C (figure 2). Increasing altitude is associated with decreasing temperature, at a rate of about 0.5°C per 100m altitude, and with increasing wind speed and day–night thermal amplitude (e.g., Mt.Catedral, 41°10'S–71°20'W, 1,450m, 1,467mm, 2.4°C). Above 2,000m altitude in the extreme north and 1,000m in the extreme south, precipitation mainly falls as snow. Microclimates are variations of these general conditions, mainly controlled by the complex and heterogeneous topography, as exposed slopes versus protected valley–bottoms, or dry north–facing slopes versus moist south–facing slopes.

Geological setting

The main physiographic units within the biome are aligned along a north–south direction. From east to west the Patagonian Plain ("Meseta Patagónica"), the Andes Range ("Cordillera de los Andes"), the Central or Longitudinal Valley ("Valle Central"), and the Coastal Range ("Cordillera de la Costa") are found (figure 1). The Patagonian Plain in the proximity of the Andes is formed of enclosed basins, either behind dams of glacial sediments or eroded by subglacial processes. The Andes from 35°S southward exhibits a lower and narrower topography in comparison with that occurring farther north. The mean maximum altitudes are dominated by volcanoes at around 2,000m above sea level, though some of them rise up to 3,500m (e.g., Mt.Tronador, 3,554m). This range is composed of intrusive volcanic granites and basalts, and of marine sedimentary rocks, which come from the late Mesozoic through the Cenozoic. The Central Valley that lies

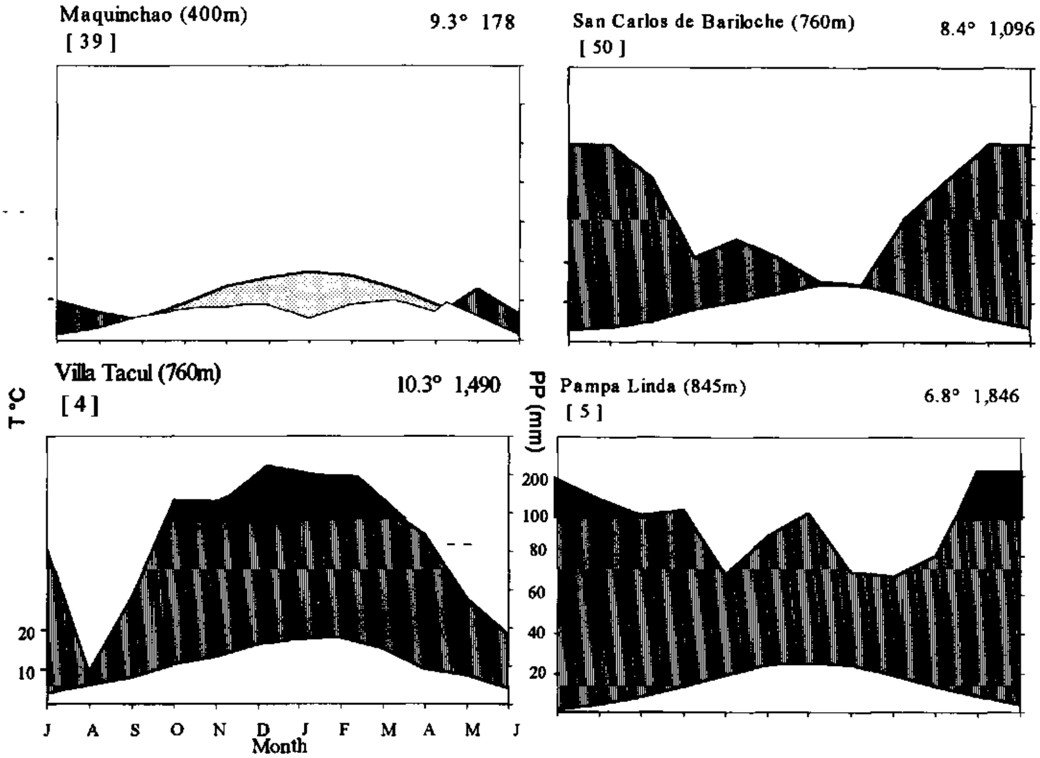


Figure 2: Climatic diagrams reflecting the west-east environmental gradient in northwestern Patagonia, Argentina. The locations (ordered by longitude) Maquinchao (41°15'S-68°44'W), San Carlos de Bariloche (41°09'S-71°18'W), Villa Tacul (41°03'S-71°34'W), and Pampa Linda (41°41'S-71°45'W) are depicted. Climate is represented by ombrothermic diagrams of Gaussen (1954), as used by Walter (1977).

between both ranges represents a subsidence zone filled up by eolic, glacial, fluvioglacial, and volcanic sediments from the adjacent cordilleras. Here, the landscape is dominated by moraine arcs, lakes of glacial origin, and fluvioglacial plains formed during past cold climatic phases. The Coastal Range is a narrow and low mountainous chain of 1,500m maximum altitude, extending along the Pacific ocean from southern Perú to middle Chile at 47°S. It is mainly conformed by metamorphic rocks from the Palaeozoic basement, and by intrusive and sedimentary rocks from the Tertiary and Quaternary. Their peneplains are dissected by profound valleys and show tectonic rising.

The landforms of the southern Andes bear the imprints of glaciation and tectonic movements that occurred along the Quaternary (Clapperton 1993, Veit & Garleff 1995). During cold phases, vast mountain icecaps developed and discharged large piedmont glaciers towards the lowlands at both sides of the Andes divide. Even where the elevation of the Andes is relatively low, some of the volcanic cones are covered by permanent snow and glaciers dominate the surroundings. Between 38° and 46°S, the climate permits the development of large ice fields on the volcanic massifs, together with smaller glaciers on mountains outside the ice field areas. For instance, the Continental Ice Field covers some continuous 20,000km^2 (figure 1). Landforms are also modelled by geocryogenic activity, a geomorphologic process distinctive of cold climates consisting in the periodic freezing and thawing of water that causes rocks to weather. Unconsolidated deposits range from till and glaciofluvial outwash, to glacio–lacustrine silt and clay of cryogenic origin. The most widespread glacial landforms are cirques, horn peaks, U–valleys, moraines, and outwash fans and terraces caused by bedrock crushing and clast entrainment. South of 43°S on either side of the mountain range, the icefield contains one of the largest and most complete moraine systems in the world, enclosing glacially eroded basins at present filled by lakes. These are true glacial lakes in the sense that water became confined into a watershed between terminal moraines. The water bodies were receding and today represent comparatively smaller remnants of former extensive palaeolakes. Glaciers at the mid–latitudes reached their Last Glacial Maximum limits at ca.18,000 years before present (yr BP) (Mercer 1984). From 16,000 to 13,000 yr BP, glaciers receded in more than half their former extension (Mercer 1984, Rabassa & Clapperton 1990).

The subsidence of the oceanic Nazca and Antarctic crust plates beneath the continental South America crust plate provides the conditions for earthquake and fire events since the Miocene. Both processes exert a primary influence on the geomorphology of the southern Andes. For instance, there was a devastating earthquake sequence in May 21 and 22, 1960, centred in Chile between 37° and 48°S. It measured 8.5 on the Richter scale, and involved both an uplift of the continental shelf by 5 to 7m, and a subsidence of the Coastal Range by 2 to 3m. These geological events are associated with extensive mass movement along steep slopes, aggravated by continuous and torrential rainfall. The southern Andes exhibits a much higher level of current volcanicity that the region farther north, and at present contains more than thirty active volcanoes (González Ferrán 1985, *ex* Clapperton 1993). Between 38° and 42°S, volcanism is predominantly basaltic as volcanoes erupt basalt and basaltic andesite, whereas south of 42°S is mainly mafic. Volcanic ash is spread all over the region. More recent pyroclastic materials, deposited by a different and multiple processes (e.g., direct deposition, volcanic loess, fluvial and glacial deposition), are situated south of 36°S (Mella & Kuhne 1985, *ex* Veit & Garleff 1995). These deposits are commonly stratified with alternate band of materials, which indicate successive and continuing eruptions. These sediments constituted the parent material for the development of the various volcanic soils types pervading the subantarctic region.

Floristic composition

The western coast of southern South America is occupied by cool–temperate rainforests. Cool–temperate rainforests develop in low– and mid–elevation extra tropical areas strongly influenced by perhumid, non–seasonal, equable oceanic climates, with an annual precipitation exceeding 1,400mm, a summer rainfall comprising at least 10% of the total annual, and a mean summer temperature reaching 16°C or lower (Alaback 1991). This forest biome also occurs at high latitudes in the Pacific Northwest of North America within the northern hemisphere, and the western coasts of New Zealand and Tasmania within the southern hemisphere. North American temperate rainforests are primarily dominated by gymnosperms. Deciduous angiosperms constitute conspicuous trees only in specialised habitats and at early stages of succession, while evergreen angiosperm trees tend to be absent (Franklin 1988, Kuiper 1994). Conversely, the temperate rainforests of the southern hemisphere are mainly dominated either by evergreen angiosperms or gymnosperms, or are composed of a mixture of conifer and broadleaved associations. Here, ecological conditions differ from those found in the northern hemisphere because of the comparatively much higher proportion of sea to land. Another cause are the humid storms, which bring constant rainfall on west–facing coasts. In consequence, at relatively mid–latitudes a humid climate persists whereas in the northern hemisphere a drier condition prevails (e.g., mainland Australia reaches 35° to 38°S, Tasmania 42°S, and New Zealand 45°S; only South America reaches a genuinely high latitude at 55°S).

The southern hemisphere biome is characterised by communities exhibiting a higher diversity in plant life forms and species than its northern hemisphere counterpart. For instance, at 41°N, 17 tree species are recorded, whereas 43 are found at the same latitude in South America (Alaback 1991). This interhemispheric pattern of plant diversity is explained by the contrasting abundance of the angiosperm component, the divergent Pleistocene histories, and the different nature of the ecotone between forests and other vegetation types (Arroyo et al. 1996). In the southern rainforests, there is a significant contribution of woody and herbaceous vines, epiphytic pteridophytes and angiosperms, and non–vascular plants. In virgin stands on optimum sites, shrubs tend to be scarce because of the dense understorey of shade–tolerant trees that develops underneath the tall, closed, multilayered forest canopy. Even though many families are well represented, the monotypic Nothofagaceae is dominant throughout the biome (table 12). From the 5 families, 33 genera, and 198 species of gymnosperms distributed in the southern hemisphere, around 36 species in 4 families, all conifers, are found in habitats within the cool–temperate rainforests (Cassie 1954, Enright et al. 1995, Biswas & Johri 1997) (table 13).

Eighteen genera of dominant, subdominant, and understorey woody plants show a wide geographical disjunction in southern South America, Australia (mainland and Tasmania), and New Zealand, as *Araucaria* (Araucariaceae), *Eucryphia* (Eucryphiaceae), *Nothofagus*, and *Podocarpus* (Podocarpaceae), according to Arroyo et al.(1996). Furthermore, close relationships exist between the Cupressaceae *Austrocedrus* (Argentina and Chile) and *Libocedrus* (New Zealand) as they were in one unique genus until recently, see Florin & Boutelje (1954), and between the monimiaceous trees *Laureliopsis* (Argentina and Chile) and *Atherosperma* (Australia) (Arroyo et al. 1996). The great similarity among the extant and fossil flora of these distant lands, including Antarctica, is a

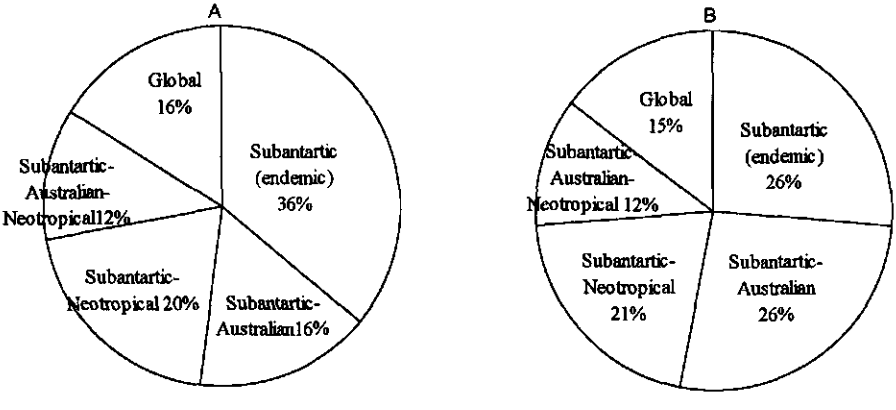


Figure 3: Biogeographical origin of the tree genera (A) and species (B) of the subantarctic forests of South America.

Table 12: The worldwide distribution of *Nothofagus* species. They are arranged according to the following subgenera (Hill & Read 1991, Hill & Jordan 1993): L= Lophozonia, B= Brassospora, F= Fuscospora, and N= Nothofagus.

Region	Species	Perennials	Deciduous	Subgenus	Species
Australia – Tasmania	3	2	1	2L+1F	*N.cunninghamii, N.moorei, N.gunnii*
New Guinea – New Caledonia	19	19	0	19B	*N.aequilateralis, N.balansae, N.baumanniae, N.brassii, N.carrii, N.crenata, N.codonandra, N.dioscoidea, N.flaviramea, N.grandis, N.nuda, N.perryi, N.stakenborghii, N.pseudoresinosa, N.pullei, N.resinosa, N.rubra, N.stylosa, N.womersleyi*
New Zealand	4	4	0	3F+1L	*N.fusca, N.solandri, N.truncata, N.menziesii*
South America	9	3	6	1F+3L+5N	*N.alessandrii, N.glauca, N.nervosa, N.obliqua, N.antarctica, N.betuloides, N.dombeyi, N.nitida, N.pumilio*
Total	35 (100%)	28 (80%)	7 (20%)		

consequence of the past interchange of biota (figure 3). It took place via terrestrial connections that existed throughout the Mesozoic, and until the Eocene (early Tertiary), around 36 Ma (Dalziel 1992). There were also long–standing terrestrial links between the tropical and temperate areas within South America, and between South America and Africa (Beard 1990). Even though Africa and South America composed the single isolated palaeocontinent West Gondwana until the early Cretaceous (135 Ma), the common biota at that time began to diverge and developed autogenously as they were influenced by different geological, climatic, and ecological events; hence a low level of phylogenetic affinity is found (Coetzee 1993, Goldblatt 1993). The southern Africa arborescent flora of Gondwana origin is represented only by a few conifers (only *Afrocarpus* and *Podocarpus* within Podocarpaceae, and *Widdringtonia* within Cupressaceae) and angiosperms, while no fossil or extant *Nothofagus* are found there (Goldblatt 1993).

In southern South America, twenty–two woody genera of flowering plants, and all the seven genera of rainforest gymnosperms have their origin in southern Gondwana, representing around 34% of the total woody genera of the region (Arroyo et al. 1996). Around 19 woody genera of plants present within the rainforests exhibit a centre of origin in the Neotropics, occurring in woodlands either in subtropical or in tropical latitudes (e.g., *Dasyphillum* (Asteraceae), *Drimys*, *Schinus* (Anacardiaceae)). These figures represent 25% of all woody genera from this region (Arroyo et al. 1996). The Neotropical genera show a biogeographical pattern characterised by the absence from the Amazon basin, and by the presence of disjunctions of southern South America with NE Argentina–SE Brazil (e.g., the tree genera *Araucaria* and *Azara* (Flacourtiaceae)) and with the tropical Andes (e.g., the bamboo *Chusquea* (Gramineae), and the tree *Dasyphillum*). The disjunction occurs at intraspecific level (e.g., the arborescent *Maytenus boaria* (Celastraceae)) or at interspecific level (e.g., the woody *Myrceugenia* (Myrtaceae)). The low–latitude species of these disjunct genera frequently occupy cool, montane habitats. The Andes probably acted as a mountainous corridor for the north– and southward movements of flora as the woody *Berberis* (Berberidaceae), *Empetrum* (Empetraceae), and *Ribes* (Saxifragaceae) (Arroyo et al. 1996). Other floristic elements from adjacent vegetation types possibly migrated into the rainforest and diversified locally. At the end of the Cenozoic, southern South America became progressively isolated because of the uplift of the Andes (early Miocene) and the development of the Humboldt cold oceanic current. Both events promoted the creation of surrounding arid environments that acted, together with the extensive water

Table 13: Geographical distribution of the 36 conifer species within the temperate rainforests of the southern hemisphere. This figure represents a 6.4% of the 559 world conifer species. Numbers between brackets indicate genera and species richness in each category (Welch 1991, Gibson et al. 1995, Odgen & Stewart 1995, Arroyo et al. 1996).

Family	**Region**		
	New Zealand (10, 20)	**South America (7, 8)**	**Tasmania (6,8)**
Araucariaceae (2,2)	*Agathis australis*	*Araucaria araucana*	----
Cupressaceae (5,6)	*Libocedrus bidwilli*, *L.plumosa*	*Austrocedrus chilensis*, *Fitzroya cupressoides*, *Pilgerodendron uviferum*	*Diselma archeri*
Podocarpaceae (11,25)	*Podocarpus hallii*, *P.totara*, *P.acutifolius*, *P.nivalis*, *Prumnopitys ferruginea*, *P.taxifolia*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Halocarpus kirkii*, *H. bidwillii*, *H.biformis*, *Lagarostrobos colensoi*, *Lepidothamnus intermedius*, *L.laxifolius*, *Phyllocladus aspleniifolius*, *P.glaucus*, *P.trichomanoides*.	*Podocarpus nuvigena*, *P.saligna*, *Prumnopitys andina*, *Saxegothaea conspicua*	*Lagarostrobos franklinii*, *Microcachrys tetragona*, *Microstrobos niphophilus*, *Phyllocladus asplenifolius*
Taxodiaceae (1,3)	----		*Athrotaxis cupressoides*, *A.laxifolia*, *A.selaginoides*

masses, as strong migration barriers. Consequently, its biota evolved independently from other tropical and subtropical forest formations of the continent.In southern South America, *Nothofagus* is the most abundant tree genus with 9 species (table 14), and Myrtaceae is the largest family of native woody perennials with 15 species (table 15). A remarkably high diversity is represented by 443 vascular plant species within 205 genera and 96 families, from which 82 genera and 160 species are woody (Arroyo et al. 1996; table 16). Around 34% of the woody genera and the entire monotypic family Aextoxicaceae are regionally endemic; in Argentina 27% of the native tree genera are endemic (table 15). Around 80% of these endemic woody genera are monotypic, and some of them comprise ancient or evolutionary relics, taxonomically isolated groups such as Gomortecaceae, Aextoxicaceae, and Misodendraceae, the hemiparasite family living exclusively together with *Nothofagus* (Arroyo et al. 1993). A remarkable level of animal biodiversity and endemism is found here as well. For instance, from 147 indigenous species of vertebrates 44.9% are endemic, whereas the amphibians represent the group comprising the highest level of endemism (80% of the total species, Armesto et al. (1995)).

Vegetation types

Phytogeographically, the temperate rainforests from South America are indistinctly named "Bosques Andino–Patagónicos" (Andean–Patagonic Forests, Dimitri 1972), "Bosques Subantárticos" (Subantarctic Forests, Alfonso 1940), "Bosques Meridionales de Sudamérica" (Meridional Forests of South America, Hueck 1978), or "Temperate Broadleaved Evergreen Forests of South America" (Veblen et al. 1983, Archivold 1995). They stretch along a narrow fringe over extensive altitudinal (0–2,000m) and latitudinal (37°45'–55°S) ranges at both sides of the southern Andes, in both Chile and Argentina (figure 1). To the north it borders on the sclerophyllous vegetation developed under a Mediterranean type of climate, which intergrade to the Atacama desert, to the east on the extensive cold and dry Patagonian steppe, and to the south and west on the Antarctic and Pacific oceans, respectively (figure 1). From north to south, there is a trend towards a decreasing richness in species and life–forms, tree dominance, and structural complexity (abundance, plant height, vertical layering) (figure 4). Tree species show a relatively large latitudinal dispersion, with a mean of 10.2° latitude, and a range of 2.1–21.8° (Arroyo et al. 1993). On the Chilean side of the Andes, the northernmost tree with a subantarctic affinity *Nothofagus obliqua* occurs at around 32°50'S, whereas on the Argentinean side it appears at 36°50'S (figure 1, table 12). This distribution reflects the different northernmost expansion of the winter–rain climates, which are linked to the circulation pattern of the westerlies (Markgraf 1987). Conifers form either monospecific stands restricted to suboptimal sites, such as *Araucaria araucana*, *Fitzroya cupressoides*, and *Pilgerodendron uviferum* (Cupressaceae), or associations primarily dominated by angiosperm trees, such as *Podocarpus nuvigena* and *Saxegothaea conspicua* (Podocarpaceae). As a broad pattern, evergreen trees are dominant where a relative climatic mildness is present as along coastline and inland zones at low elevations, while deciduous trees where a greater winter harshness, continentality, or seasonality prevails (Chinese *Fagus* species show a comparable distribution as shown by Cao et al. (1995)). However, there are also many mixed deciduous–evergreen associations, such as those composed of *Nothofagus nervosa*, *Nothofagus obliqua*, and *Nothofagus dombeyi*. Frequently there are also imprecise limits between deciduous and evergreen stands, as between *Nothofagus pumilio* and *Nothofagus betuloides*. Apart from the leaf habit, other plant adaptations influence species

Table 14: Characteristics of the *Nothofagus* tree species from South America.

Species	Subgenus[1]	Distribution		Regeneration[4]	Leaf[5]								Flower[6]				Fruit		Hybrids[10]	Vegetative propagation	Parasite	
		District[2]	Range[3]		Vernation	Type	Size	Width/length (cm)	Form	Texture	Margin	Serration	Valves (n°/cupule)	Stamens (n°/cupule)	Perianth□	Pollen[7]	Weight[8] (gr/1,000 fruits)	Type[9]			*Cyttaria*[11]	*Heterobathmia*[12]
N.alessandrii	F	M	C: 35°05-35°49'S	nd	nd	d	b	2.5 – 9.0 4.5 – 13.0	sm	ca	se	c	4s	<20	t	Nf_a	7.5- 13.2	A	nd	nd	–	no
N.antarctica	N	R	A: 38°00'–55°30'S C: 35°31'–55°30'S	r	Pi	d	s	1.3 – 2.5 1.8 – 4.5	sm	ca	de	c	4s	<20	t	Nf_b	1.5 – 3.1	B	nd	yes	2,4,5	yes
N.betuloides	N	M	47°00'–55°30'S	g	Pl	e	s	1.0 – 2.0 1.5 – 3.5	sm	co	se	s	4s	<20	t	Nf_b	1.9 – 2.4	B	γ δ	no	2,3,4 5,6	no
N.dombeyi	N	VP	A: 38°00'–44°00'S C: 34°40'–47°30'S	r	Pl	e	s	0.7 – 1.5 2.0 – 2.5	as	co	se	s	4s	<20	t	Nf_b	0.6 – 4.4	B	δ σ	no	4,6	no
N.glauca	L	M	C: 32°00'–36°30'S	nd	nd	d	b	3.5 – 5.0 4.5 – 7.0	as	ca	de	c	4s	>20	o	Nm	357 – 705	B	α	yes	1	no
N.nervosa	L	V	A: 39°22'–40°23'S C: 35°20'–41°30'S	r	Pi	d	b	1.0 – 3.0 3.0 – 12.0	sm	ca	de	c	4s	>20	o	Nm	3.8 – 13.3	B	β	yes	7	yes
N.nitida	N	VP	C: 40°20'–48°30'S	r	Pl	e	s	1.5 – 2.5 2.0 – 3.5	sm	co	se	sc	4s	<20	t	Nf_b	0.7 – 0.9	B	γ σ	no	4	no
N.obliqua	L	V	A: 36°50'–40°15'S C: 32°50'–41°30'S	r	Pi	d	b	1.5 – 3.0 2.5 – 6.0	as	ca	se	c	4s	>20	o	Nm	7.0 – 24.4	B	α β	yes	1,7	yes
N.pumilio	N	R	A: 36°56'–55°30'S C: 35°30'–55°30'S	g	Pi	d	s	1.0 – 1.7 1.5 – 3.0	sm	ca	de	s	2a	<20	t	Nf_b	20.4	C	nd	yes	2,4,5	yes

(1)F: Fuscospora, L: Lophozonia, N: Nothofagus (from Hill & Jordan 1993). (2) M: Mesophytic Temperate Forests, RF: All Rainforests districts, V: Valdivian RF, P: Patagonian RF, M: Magellanic RF (following Veblen et al.1983). (3) Trees are spread along the southern Andes between the indicated latitudes. In the northern extreme *N.obliqua* var.*macrocarpa* is found. A: Argentina. C: Chile. (4)Regeneration modes (RM)= r: stand replacement RM, g: fine–scale gap RM, nd: not determinated (Veblen & Alaback 1996). (5)d: deciduous, e: evergreen; b: big, s: small; as: asymmetrical, sm: symmetrical; ca: cartaceous, co: coriaceous; se: serrate, de: dentate; c: composite, s: simple; Pl: plane, Pi: plicate (Philipson & Philipson 1979, Romero 1980). (6) Female flowers are grouped in a cupule formed by a peduncle with 2 or 4 valves. 4s: symmetrical cupule with 4 valves. 2a: asymmetrical cupule with 2 valves; >20: more than 20 stamens per male flower, <20: fewer than 20 stamens per male flower; t: male perianth a tube. o: male perianth open. (7)Nm: *N.menziesii* type (pollen colpi with annulate thickening), Nf_a: *N.fusca* type a (pollen colpi rimmed), Nf_b: *N.fusca* type b (pollen colpi unthickened)(Dettmann et al.1990). (8) According to Burschel et al.1976, Donoso & Cabello (1978), Ordoñez (1987), Rodríguez (1990), Santelices et al.(1996), Marchelli & Gallo (1999). (9)A: 7 fruits per cupule, 1 central dimerous and 6 laterals trimerous; B: 3 fruits per cupule, 1 central dimerous and 2 laterals trimerous; C: 1 trimerous fruit per cupule. (10)Same letters indicate natural hybridisation between species; nd= not determinate (Donoso & Landrum 1979, Lennon et al.1982, Donoso & Atienza 1983,1984, Donoso et al.1990).(11) Genus of 11 gall–forming phytoparasitic fungi exclusive in the temperate species of *Nothofagus*. 1: *Cyttaria berteroi*, 2: *C.darwinii*, 3: *C.exigua*, 4: *C.harioti*, 5: *C.hookeri*, 6: *C.johowii*, and 7: *C.spinosae* (Gamundi 1971, Humphries et al.1986). (12)Genus of primitive Lepidoptera whose larvae are miners in newly set leaves of deciduous *Nothofagus*. Around 10 species are identified (Kristensen & Nielsen 1983).

Table 15: Woody plants from the temperate rainforest of South America.

Trees (1)						Shrubs (4)
Range (2)	Family	Genus	Species	Height	Total (3)	
Subantarctic A 9 (27%)	Aextoxicaceae (a)	*Aextoxicon*	*A.punctatum*	β	1	*Acrisione, Asteranthera, Notanthera, Ovidia, Boquila, Campsidium, Latua, Desmaria, Elytropus, Ercilla, Philesia Lapageria, Lardizabala, Lebetanthus, Mitraria, Misodendrum, Myoschilos, Sarmienta, Tepualia*
	Myrtaceae	*Amomyrtus*	*A.luma*	α	2	
		Myrceugenella	*M.apiculata* (c)	β	2	
	Cupressaceae	*Austrocedrus*	*A.chilensis* (c)	δ	1	
		Fitzroya	*F.cupressoides* (c)	γ	1	
		Pilgerodendron	*P.uviferum* (c)	γ	1	
	Proteaceae	*Embothrium*	*E.coccineum*	α	1	
	Monimiaceae	*Laureliopsis*	*L.philippiana*	δ	1	
	Podocarpaceae	*Saxegothaea*	*S.conspicua*	δ	1	
Subantarctic Australian B 9 (27%)	Eucryphiaceae	*Eucryphia*	*E.cordifolia*	δ	5	*Aristotelia, Discaria, Hebe, Sophora Luzuriaga, Muehlenbeckia,*
	Proteaceae	*Gevuina*	*G.avellana*	β	3	
	Nothofagaceae	*Nothofagus* (c)	*N.antarctica* (b), *N.dombeyi*, (b) *N.pumilio* (b), *N.obliqua* (b), *N.betuloides*, (b) *N.nervosa*	α-γ	35	
	Araliaceae	*Pseudopanax*	*P.laetevirens* (b)	β	6	
Subantarctic Neotropical C 7 (22%)	Flacourtiaceae	*Azara*	*A.lanceolata,* *A.microphylla*	β	10	*Adesmia, Antidaphne, Myrteola, Ugni, Fuchsia, Blepharocalyx, Tristerix, Chusquea, Chiliothrichum, Mutisia, Crinodendron, Desfontainea, Hydrangea, Escallonia, Lepidoceras, Raphithamnus*
	Asteraceae	*Dasyphyllum*	*D.diacanthoides*	α	36	
	Winteraceae	*Drimys*	*D.winteri*	β	6	
	Myrtaceae	*Myrceugenia*	*M.chrysocarpa,* *M.exsucca*	β	40	
	Anacardiaceae	*Schinus*	*S.patagonicus* (c)	α	27	

Table 15 (cont.).

Subantarctic Australian Neotropical D 4 (12%)	Araucariaceae	*Araucaria*	*A.araucana* (c)	γ	18	*Griselinia*
	Proteaceae	*Lomatia*	*L.hirsuta,* *L.ferruginea*	β	5	
	Podocarpaceae	*Podocarpus*	*P.nuvigena*	δ	70	
Global E 5 (12%)	Cunoniaceae	*Caldcluvia*	*C.paniculata*	β	11	*Blechnum, Baccharis, Berberis, Buddleja, Cissus, Ribes, Ephedra, Rhamnus, Coriaria, Empetrum, Solanum, Senecio, Pernettya, Corynabutilon, Gaultheria, Prumnopitys*
		Weinmannia	*W.trichosperma*	β	150	
	Celastraceae	*Maytenus*	*M.boaria* (c), *M.magellanica*	α	225	
	Lauraceae	*Persea*	*P.lingue*	β	150	

A: Monospecific genus endemic from the temperate rainforests (TRF) of southern South America. B: Genus distributed in (A) and Australia (mainland and Tasmania), New Zealand, New Guinea, and New Caledonia. C: Genera distributed in South America. D: B + C. E: Cosmopolite genus. (a) Endemic family. (b) Deciduous species. (c) Species that eventually form monospecific forests. (1) Trees from the TRF of Argentina. (2) Number and percentage of species in each region are shown. (3) Total number of species is indicated. (4) Shrubs from the TRF of Argentina and Chile. α:<10m total height, β:10–20m, δ:20–30m, γ:>30m.

boundaries, like the tolerance of the evergreen *Nothofagus betuloides* and the deciduous *Nothofagus antarctica* to waterlogged soils. Veblen et al.(1983) divided the biome into three large vegetational districts: the Valdivian (37°45'–43°20'S), the Patagonian (43°20'–47°30'S), and the Magellanic

Table 16: Number of vascular plants of the temperate rainforest of southern South America (Arroyo et al. 1996).

Taxa	Families	Genera	Species (%)	
Pteridophytes	12	23	66	14.9
Gymnosperms	3	7	8	21.2
Monocotyledons	13	42	94	1.8
Dicotyledons	68	133	275	62.1
Total	96	205	443	100.0

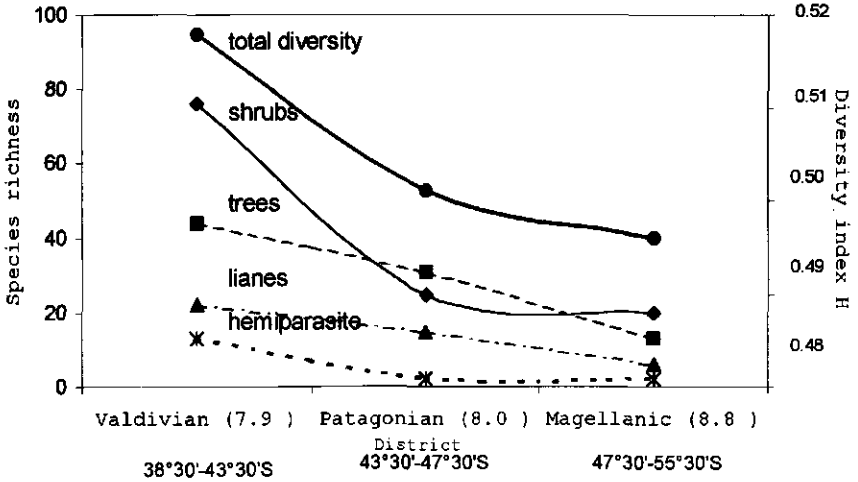


Figure 4: Species richness of life forms (primary y-axis) and total α-diversity (H) (secondary y-axis) within the phytogeographic districts of the temperate rainforests of South America. Shannon-Weiner diversity index H (Shannon & Weaver 1949)= $-\Sigma$ Pi log Pi, where Pi equals the proportional representation of each woody life form. Temperature range equals mean temperature of warmest month minus mean temperature of coolest month (between brackets). Data from Arroyo et al.(1996).

Rainforest District (47°30'–55°S) (figure 1). Exclusively in Chile between 32°–36°30'S, the Mediterranean forest conformed by *Nothofagus glauca*, *Nothofagus alessandrii*, and the hybrid *Nothofagus leonii* is found (table 14). Between 35° and 40°S, a mixed deciduous stands of *Nothofagus obliqua* and *Nothofagus nervosa* are predominant on well–drained and fertile soils at altitudes reaching 1,000m. Farther south, at altitudes bellow 400m in flat terrains or on gently slopes on humid and adequately drained volcanic soils, a multilayered forest type remarkably diverse in species and life form dominates. It is composed of broadleaved evergreen species together with Podocarpaceae and Cupressaceae conifers. *Laureliopsis philippiana*, *Eucryphia cordifolia*, *Aextoxicon punctatum* (Aextoxicaceae), and *Nothofagus spp.* are the most characteristics trees. *Persea lingue* (Lauraceae), *Drimys winteri*, *Pseudopanax lataevirens* (Araliaceae), and many myrtaceous shrubs and small trees are subdominants. Several epiphytes as bromeliads and hymenophyllaceous ferns, and very robust lianas are found. Several species of the bamboo *Chusquea* proliferate in the understorey, but become absent south of ca.48°S *Nothofagus spp.* may be locally absent within this forest type. On poorly drained, seasonally flooded sites *Nothofagus nitida*, *Laureliopsis philippiana*, *Weinmannia trichosperma* (Cunoniaceae), *Eucryphia cordifolia*, *Amomyrtus luma* (Myrtaceae), and *Drimys winteri* are the dominants. On peat and acidic soils saturated by water all year–round along river courses or on flat terrain, an azonal, mixed community occurs. It is composed of *Pilgerodendron uviferum*, *Tepualia stipularis* (Myrtaceae) and *Drimys winteri*, with an understorey frequently dominated by mosses. Many forest types of divergent species composition correspond with different successional stages: the pure *Drimys winteri* forests, the evergreen forests with only shade–intolerant trees, and the evergreen forests in which shade–tolerants appear in the composition constitute a chronosequence of the same successional process. A parallel status of apparently different forest types being successional seres was described for New Zealand temperate rainforests by Six Dijkstra (1981).

Within the Valdivian district, but at higher elevations between 400 and 1,000m, *Nothofagus dombeyi* and *Eucryphia cordifolia* are the co–dominant trees, above a subcanopy composed of *Laureliopsis philippiana*, *Dasyphyllum diacanthoides*, and *Saxegothaea conspicua*. Here, *Nothofagus dombeyi* attains its maximum diameter and height. At higher elevations between 1,000 and 1,600m, low winter temperatures and long periods of snow cover determine the development of pure stands dominated by the deciduous *Nothofagus pumilio*, extending over 2,000km from 36°55' to 55°S. This species forms the altitudinal limit of the arborescent vegetation attaining 30m height. At the tree line, however, it becomes very low and adopts the form of a dwarf shrub, with a stunted, gnarled stem. The understorey is occupied by *Chusquea tenuiflora* ("quila") in lowland areas and by *Chusquea culeou* ("caña colihue") at mid–elevations, and bryophytes and lichens commonly cover the ground. The deciduous and small *Nothofagus antarctica* exhibits an ample altitudinal distribution, covering the entire range of the biome only in marginal sites. It occurs discontinuously in pure stands, mainly in extreme sites on lava and ash deposits at very high altitudes, or on permanently waterlogged soils at different elevations. The coniferous, long–lived forests dominated by *Araucaria araucana* develop from 37°20' to 40°20'S at both sides of the Andes at altitudes between 900 and 1,800m. They are found in a moist winter and dry summer climate, either on young soils derived from recent ash deposits or on well–developed soils of non–volcanic origin. *Araucaria araucana* may form different associations together with *Nothofagus pumilio* and *Nothofagus antarctica* at high altitudes, with *Nothofagus dombeyi* at lower elevations, or with *Austrocedrus chilensis* in drier sites. In Argentina and Chile, from 39°50' to 43°30'S, the largest and longest–lived South American conifer *Fitzroya cupressoides* forms discontinuous populations at low and mid–elevations up to 1,500m. At high altitudes it may constitute pure stands mainly on thin, coarse–textured volcanic soils, whereas on swampy soils it forms mixed stands with *Pilgerodendron uviferum*. At low elevations on zonal soils, it appears sparsely as large trees within the rainforests. In Argentina, the Valdivian Rainforest is a discontinuous and poorly represented association, located in the National Parks Nahuel Huapi, Lago Puelo, and Los Alerces (Correa Luna & Dimitri 1969, Hueck 1978, Rodríguez García et al. 1978, Seibert 1982).

The Patagonian and the Magellanic Rainforest is a relatively species–poor vegetation district confined to coastal fringes, where typical lowland Valdivian species are absent. Towards the western coastal zone, moorlands composed of a mosaic of bare rock, bogs, and cushion and tussock plants become important. Patagonian Rainforest is characterised by the dominance of *Nothofagus dombeyi, Weinmannia trichosperma*, *Saxegothaea conspicua*, *Podocarpus nuvigena*, and *Drimys winteri*. On waterlogged soil, the conifer *Podocarpus nuvigena* prevails. Along the coast the evergreen *Nothofagus betuloides* characterises the Magellanic Rainforest, which extends from ca. 48° to 55°S, mostly in warmer and wetter, usually waterlogged sites. It forms pure or mixed forests particularly with *Drimys winteri*. At higher elevations and towards the eastern drier areas a transitional, mixed evergreen–deciduous *Nothofagus betuloides* and *Nothofagus pumilio* forests develop. On harsher, well–drained soils showing podzolization, *Nothofagus pumilio* is the dominant tree. Epiphytic ferns and mosses are abundant. Following the striking west–to–east precipitation gradient, there is a vegetational gradient from the species–rich temperate rainforests, through the *Nothofagus*–dominated rainforests, the mixed *Nothofagus dombeyi* – *Austrocedrus chilensis,* the *Austrocedrus chilensis* woodlands, and finally the Patagonian steppe. In the above, the analysis is limited to the context strictly necessary for the present study. A more complete description of the vegetation types is found in Dimitri (1972), McQueen (1976,1977), Hueck (1978), Veblen et al. (1983), Schmaltz (1991), and Donoso (1993).

Soils

In the Subantarctic Forests, the prevailing soil types derive from volcanic ash and therefore they have many properties in common. They are comparatively young, since most volcanic components originated from eruptions having taken place during the Quaternary. Soils are the result of weathering of both the autochthonous rocks and the allochthonous pyroclastic deposits that cover the landscape extensively. Nevertheless, the age, thickness, geomorphological position, and physicochemical characteristics of these volcanic materials were more important than the subjacent rocks for soil genesis. In southern South America, the distribution of recent and past volcanic ash and related materials commences at ca.35°S, but they form an interrupted mantle from 36°30'S southward (Wright 1965). In general, temperate soils derived from volcanic ejecta are considered very productive and fertile substrates (Miller & Donahue 1995). However, their inherent properties often change irreversibly when vegetation is not properly managed. Physical and chemical soil degradation and erosion proceed after the simplification and elimination of vegetation, which plays a relevant role in soil conservation. For instance, the direct impact of raindrops on bare surfaces during the persistent heavy rains destroys soil aggregates and so compacts the soil. Upon drying, this non–aggregated soil surface forms a barely permeable crust, so the amount of runoff water carrying soil particles increases. At the same time, a loss of diffusion capacity to gases inhibits plant germination, establishment, and growth. The climatic and geologic features make western Patagonia a region with a high intrinsic susceptibility to erosion, therefore vegetation integrity is essential for soil conservation.

Andosols (FAO–UNESCO soil classification system, FAO 1990), Inceptisols Andepts (USDA Soil Survey Staff, USDA 1975) are known locally as Trumaos, from an aboriginal word implying lightness. They extend from 36° to 50°S, covering 62% of the volcanic ash soils occurring in southern Chile (Wright 1965, Mella & Kuhne 1985, *ex* Veit & Garleff 1995). These weakly to moderately developed soils occur on glacial and fluvioglacial deposits from the last glacial period, and present ash deposition from the transition Pleistocene–Holocene (Mercer 1976). Their main properties are a high water holding capacity and permeability, a high total porosity, a low bulk density (0.6–0.9g cm^{-3}), a high level of lime (50–65%), clay (max.40%), and organic matter (12–16% C), and a moderate acidity with pH between 4.5 and 5.8 (Holdgate 1961, Veit & Garleff 1995). Amongst the amorphous clays allophane and imogolite are the dominants, causing a high cation exchange capacity (230–780cmol kg^{-1}), a high phosphate retention, and a low base saturation. Under natural vegetation they usually present a superficial horizon hosting intense fibrous root development, whereas relatively few roots penetrate into the deeper subsoil layers. Andosols develop under a humid to perhumid, cool climate, occupying almost any type of relief from the extremely pronounced slopes of the Andes to the undisturbed flat plains and terraces of the interior valleys. They extend eastward into Argentina, but their andic properties gradually diminish owing to increasing dryness and cold of the Patagonian plain. Vegetation associated to Andosols includes different types, such as mixed deciduous forests (e.g., composed of *Nothofagus nervosa* and *Nothofagus obliqua*), broadleaved evergreen rainforests (dominated by *Nothofagus dombeyi*, *Aextoxicon punctatum*, *Laureliopsis philippiana*, and *Eucryphia cordifolia*), and pure conifer or broadleaved forests (composed either of *Fitzroya cupressoides*, *Araucaria araucana*, *Nothofagus antarctica*, or *Nothofagus pumilio*).

Gleysols (FAO–UNESCO soil classification system, FAO 1990), Aquepts (USDA Soil Survey Staff, USDA 1975), are known locally as Ñadis from an aboriginal word implying swampy land. They are determined by both the parent material and the topography. Their chemical and physical properties resemble those of Andosols. However, the organic matter content is generally higher with a marked peat accumulation, and they exhibit reduction symptoms characteristic of cold and humid climates. In the boundary between the volcanic/eolic and the fluvioglacial horizons, a discontinuous layer rich in iron, manganese, and silica occurs. The maximum development of Gleysols takes place under a cool climate, with an annual rainfall exceeding 1,500mm evenly distributed along the year, on flat or very gently undulating landforms associated with glaciated landscapes, terrace formation, or lacustrine deposits. On this soil type plant species are diverse and xeromorphic features are common. Physiognomically, they form a stunted, very dense thicket composed of Myrtaceae, Ericaceae, Berberidaceae, Juncaceae, and Cyperaceae species, together with a dense undergrowth abounding in mosses and ferns. Within this soil type, mixed forests include the trees *Pilgerodendron uviferum*, *Drimys winteri*, *Nothofagus nitida*, *Laureliopsis philippiana*, *Weinmannia trichosperma*, *Eucryphia cordifolia*, and *Amomyrtus luma*. Under swampy conditions, pure forests with *Nothofagus antarctica* and *Fitzroya cupressoides* develop, whereas on areas with higher rainfall *Nothofagus dombeyi* forests arise. Nitisols (FAO–UNESCO soil classification system, FAO 1990) are palaeosoils developed from the weathering of past volcanic ash and metamorphic rocks from the Palaeozoic, and of sedimentary marine and continental rocks from the Tertiary. They may present a rejuvenation process that results from the input of modern volcanic materials. Their main properties are a high water holding capacity, a moderate acidity (pH=3.6–4), a low organic matter content, an intermediate cation exchange capacity, and an absence of allophane.

Quaternary history

The climate and vegetation during the mid– and late Quaternary has been primarily inferred by semiquantitative analysis of fossil pollen from peat samples taken between 38°S (the Lakes District) and 55°S (Tierra del Fuego island) (figure 1). The palaeoenvironmental reconstruction rests on the assumption that pollen influx to lakes or bogs reflects the dominant contemporary vegetation in the surrounding landscape, and that the communities respond to small– or large–scale climatic change. However, hypotheses on past climate and vegetation are based on limited information, collected in an extensive and complex region (Markgraf 1993). In the region, the Quaternary is characterised by alternating prolonged cold glacial and warm interglacial phases, accompanied by minor interstadial warming and stadial cold episodes. Dominant physical processes associated with this climatic fluctuation were sea– and lake–level variations, loess deposition, and glacier advance and retreat. In turn, vegetation responses included changes in abundance, range, and local and global extinction of species.

The Full Glacial of the late Pleistocene, dated around 18,000 yr BP, is characterised by a climate wetter, and about 4°–5°C cooler than today, an increased terrestrial and marine ice cover, and a decreased sea level (Markgraf 1993). At mid–latitudes in the Lakes District (38–42°S), ice–free conditions prevailed in the lowland sites, which were occupied by herbs, shrubs, and to a lesser extent by *Nothofagus*, *Podocarpus*, and *Prumnopitys* (Podocarpaceae) (Heusser 1981, Villagrán 1990). Hygrophilous forest formations built by Myrtaceae, *Nothofagus*, *Podocarpus*, *Lomatia* (Proteaceae), and *Drimys* expanded towards warmer areas, downward to the valleys and northwards. Farther south at Chiloé Island (42°–43°S), the vegetation exhibited a mosaic structure formed by patches of grasslands, moorlands, and woodlands (Villagrán 1990). *Nothofagus dombeyi* and Gramineae were the dominant plants in the Mediterranean–type as well as in the temperate region, reaching 50°S Today, moorlands, a boggy herbaceous formation dominated by cushion plants, are located along the coastline of Tierra del Fuego 6° latitude farther south, where the current highest records of rainfall and wind velocity have been measured. Chiloé island constituted a boundary between those territories that were completely glaciated to the south, and those partially invaded by glaciers to the north (Villagrán 1990). At high latitudes in the Channels District (43°–55°S), during the Last Glacial Maximum the subantarctic forest was largely devastated directly by glacier cover or indirectly by fluvioglacial activity and climatic change (Hollin & Schilling 1981). However, the region was not entirely ice–covered and the biota probably was not completely eliminated from this zone, so that it survived glaciation in Pleistocene refugia (Villagrán 1990, Ashworth et al. 1991).

After the latest advance of glaciers during the late Pleistocene, climate changed to an interglacial, major warming mode around between 12,700–15,800 yr BP depending on the latitudinal location (Mercer 1984, Porter et al. 1984, Heusser 1989, Clapperton 1990, Ashworth et al. 1991). In the Nahuel Huapi District (41°S, east of the Andes; figure 1), Rabassa & Clapperton (1990) reported that glaciers receded before 13,000 yr BP. Following deglaciation, the initial vegetation throughout southern South America was open, suggesting a widespread occurrence of low levels of rainfall and long summer moisture stress (Villagrán 1990). In the mid–latitudes a rapid and synchronic *Nothofagus* expansion began, probably from the refugia of biota located nearby the glaciated areas, while at high latitudes *Empetrum* and Gramineae heathlands were the dominant vegetation. (Villagrán 1990). The first seral successional assemblage was constituted by conifers and *Nothofagus* in montane sites, and of course more thermophilic species in lowland sites, and aquatic and swamp taxa in the wetlands (Villagrán 1990). By 12,500 yr BP, Patagonian mixed rainforests replaced the earlier open *Nothofagus* woodland in the Lakes District. During the same period in the Channels District, *Nothofagus* forests replaced heathlands. In contrast, the vegetation in Tierra del Fuego continued to be treeless until after 9,500 yr BP, although grasses replaced *Empetrum* dominated–communities at about 12,500 yr BP implying a trend to more mesic conditions (Rabassa & Clapperton 1990).

During the early Holocene (10,000–5,000 yr BP) there was a general trend towards a warmer climate. In the Lakes District, this period is characterised by the expansion of more thermophilic Valdivian tree species that replaced the Patagonian Rainforest species. The deciduous *Nothofagus nervosa* and *Nothofagus obliqua* that dominated the montane environments were replaced by Patagonian Rainforest taxa and retreated to the north, gradually occupying their present range (Heusser 1984). Farther south, the Channel District was characterised by the presence of a rainforest–moorland mosaic. In the south–eastern Andes, at around 9,500 yr BP, *Nothofagus* forests began to expand simultaneously at several sites indicating that precipitation had increased as well, although the relative openness of these forests suggest that moisture then was lower than today (Markgraf 1983). At mid–Holocene (5,000–3,000 yr BP) a more xeric climate prevailed all over the subantarctic region. An expansion of the steppe towards the eastern foothills and a replacement of evergreen by deciduous trees at the western foothills occurred. In eastern Tierra del Fuego, expansion of grasses and herbs occurred between 6,000–5,000 yr BP (Markgraf 1983). In the Beagle Channel (55°S) the *Empetrum*–dominated heathlands expanded between 5,500–4,000 yr BP (Heusser 1989, Markgraf 1989). In Southern South America, the establishment of the modern climatic regime, characterised by warmer temperatures and higher levels of precipitation, occurred by 3,000 yr BP when the current major vegetational zonation was conformed.

Ecological impacts

In the subantarctic region, natural ecological impacts are frequent and exert an important influence on the prevalent pattern and dynamics of forests. Large–scale impacts are mainly geological (e.g., earthquakes, volcanism) and climatological (e.g., glaciation). Geological events are frequent as a results of the convergence of crust plates. Earthquakes are associated with extensive mass movement along steep slopes in the form of debris and snow avalanches, landslides, and mudflows, aggravated by continuous and torrential rainfalls. They cause direct elimination of entire stands, increase in treefall rates by intense shaking on unconsolidated debris, and changes in the growth pattern of surviving individuals (Veblen & Ashton 1978, Veblen et al. 1992a, Kitzberger et al. 1995). Land subsidence caused by earthquakes also promotes inundation and massive mortality of coastal Patagonian and Magellanic Rainforests (Goodall 1979). In the southern Andes, there are numerous active volcanoes whose lava flows have devastated large tracts of natural forests at both sides of the divide (Veblen & Ashton 1978). Without subsequent abiotic impacts, secondary succession on bare soil or on recently deposited lava and ash materials involves the re–occupation of the sites by light–demanding trees (e.g., *Nothofagus spp.*, *Fitzroya cupressoides*). Otherwise, they tend to be replaced by shade–tolerant trees (Burschel et al. 1976, Veblen & Ashton 1978, Veblen et al. 1981, Veblen 1982, Donoso et al. 1984, 1985, Armesto & Figueroa 1987, Armesto & Fuentes 1988). Active glaciers are common in the southern Andes. *Nothofagus* and other light–demanding trees become established in even–aged populations on stabilised moraines rapidly after glacial retreat, or even on in–transit moraines where soil materials have been deposited over the surface of glacial ice (Veblen et al. 1989a). Post–glacier primary succession is comparatively more rapid than in other biomes, because of the mild climate and the available water (Veblen & Alaback 1996). Mortality of individual trees or stands is frequently caused by strong winds acting on shallow rooted *Nothofagus* species.

The optimal physical setting for the extensive development of cool–temperate rainforest occurs in south–central Chile, a region in which the European colonisation took place early. Before the sixteenth century, aborigines lived in transient areas along the edges of forests and lakes, exhibited a hunter–gatherer organization with a rudimentary agriculture, and utilised small quantities of wood for cooking, heating, and for construction of shelters, canoes, and armaments (Donoso & Lara 1995). With the beginning of the Spanish colonisation of southern Chile in 1552, aborigines were forced to retreat farther south. The territory located between 37°–40°S remained under aboriginal control until 1888. South of 40°S, extensive areas for agriculture and cattle raising were established in former forested lands, whereas in other timber extraction for ship construction and fuel occurred. *Austrocedrus chilensis*, *Drimys winteri*, *Nothofagus obliqua*, and *Fitzroya cupressoides* were the most affected species by selective or clear–cutting, for a large ship building industry. In the mid–nineteenth century, massive forest destruction took place because of the successive arrival of colonists from Germany, Switzerland, and Italy. Clear–cutting of stands and selective cutting of the best individuals of the most valuable species, particularly of *Nothofagus nervosa* and *Fitzroya cupressoides*, was very intense. Old–growth forests comprising *Nothofagus spp.* and many other species were extensively clear–cut or burnt for land conversion. Some fires lasted several months without any control, crossing the Andes following the dominant wind direction, then burning thousands of hectares of Argentinean woodlands (Willis 1914, Rothkugel 1916). Forest exploitation of the species–poorer Patagonian Rainforest occurred since the beginning of the twentieth century, particularly affecting the deciduous *Nothofagus pumilio* and the high–quality timber *Pilgerodendron uviferum*. The southernmost part of South America, where the Magellanic Rainforests prevail, exhibits a very sparse human population and forests remain practically intact.

At present, only 9% of the land under the Chilean natural reserve jurisdiction is occupied by native forests, and the rate of forest degradation and lost is estimated to be 120,000ha yr^{-1} (Lara et al. 1995). Only between 2,700 to 5,000ha of natural forested lands are managed under schemes of sustainability (Ormazábal 1992, *ex* Lara et al. 1995). Forest is the primary source for woodfire, charcoal, and cellulose, and the quantity of extracted timber volume increased threefold during 1988–1990 (Lara et al. 1995). The disappearance of forest is also related to land conversion from woodlands to plantation, mainly with fast–growing conifer and broadleaved exotics (e.g., *Pinus radiata, Pseudotsuga menziesii, Eucalyptus globulus* (Myrtaceae)). During 1974–1992, more than 200,000ha of native forests were replaced by plantations that attained 1,5 million hectares (Lara et al. 1995). Anthropogenic fires devastate an impressive area each year, particularly in unusually dry summers. During the summer of 1990–1991, more than 45,000ha of native vegetation were completely burnt. The effect of forest exploitation is that 28 tree species are classified as vulnerable or in danger of local extinction, such as *Saxegothaea conspicua* and *Weinmannia trichosperma* (Benoit 1989). The long–lived, slow–growing native conifers *Araucaria araucana* and *Fitzroya cupressoides*, which formerly occupied large areas, have been included in the Appendix 1 of the Convention on International Trade in Endangered Species (CITES). *Fitzroya cupressoides*, with an individual older than 3,600 years (Lara & Villalba 1993), ranks second among long–lived organisms on Earth.

In Argentina, fires constitute an important impact on vegetation. The fire regime has changed along spatial and temporal scales, reflecting the interplay among human activities, differential fire–proneness, climate seasonality, and interannual variations (Kitzberger et al. 1997). Forest fire frequency increased dramatically around 1850, reached a maximum in 1890, and then followed a decline throughout the 20th century (Veblen et al. 1999). During the aboriginal settlement period, before ca.1880, inhabitants caused many fires along the forest/steppe ecotone, basically as a tool for hunting the native Camelidae *Lama guanicoe* (Eriksen 1975, Veblen & Lorenz 1987, 1988). In moist forests occurring towards the west fires were infrequent but caused massive mortality (Kitzberger et al. 1997). During the European settlement period from 1880 to 1930, the burning frequency in the transitional zone decreased as a result of the drastic elimination of the Indian population. On the contrary, in the densely forested areas towards the west, early European colonists cleared lands to expand pastures and, to a lesser extent, to permit agriculture and access to timber species (Willis 1914, Rothkugel 1916, Tortorelli 1947). In northwestern Patagonia, about 693,000ha from a total of 1,873,000ha of woodlands were burnt during that period (Rothkugel 1916). During the post–settlement period, after 1930, many natural reserves were created (the Nahuel Huapi National Park in 1934), several forest laws were promulgated (The Forest Richness Law in 1948), and rural population became stabilised. These measures promoted forest fire suppression throughout the region

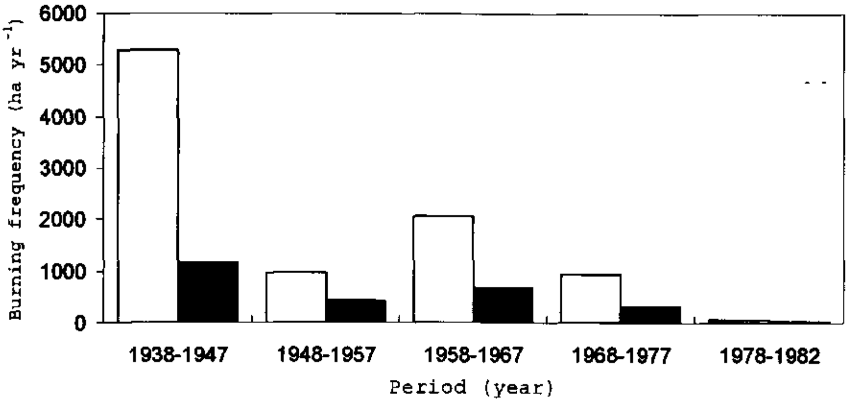


Figure 5: Fire frequency affecting all forest types (empty bars) and forest types dominated by *Austrocedrus chilensis* (shaded bars) in the natural reserves of northwestern Patagonia, Argentina, during 1938-1982 (data from Bruno 1982).

(figure 5). In *Austrocedrus chilensis* stands, the mean interval between fires was 16.5 years during fire exclusion (1930–1989), compared to 2.2 years for the preceding period (1880–1929) (Veblen et al. 1999). This is reflected in the common occurrence of even–aged, single cohort stands of *Austrocedrus chilensis* and *Nothofagus dombeyi* of 70 to 120 years old (Veblen & Lorenz 1988, Veblen et al. 1992a).

At present, forests are cleared for real state development and illegal timber extraction, given a urbanisation process of many cities located along the annual isohyets of 1,000mm (Eriksen 1970). The urban fringe of such rapid population growth (San Carlos de Bariloche doubles its population every 12.4 years (Dezzotti & Sancholuz 1999)) overlaps with the natural range of several forest types. Forests are also very sensitive to the presence of domestic livestock (Lebedeff 1942, Tortorelli 1956, Costantino 1958, Thomasson 1959, Anziano 1962, Daciuk 1973, Muttarelli & Orfila 1973). Other introduced animals, such as deer (*Cervus elaphus*, *Dama dama*, and *Axis axis*), hares (*Lepus europaeus*), boars (*Sus scrofa*), rabbits (*Oryctolagus cuniculus*), and beavers (*Castor canadensis*), are particularly damaging (Goodall 1979, Bava & Puig 1992, Veblen et al. 1989b, 1992b, CIEFAP 1993). Direct and indirect effects of introduced large animals are related to the inhibitory effect on tree regeneration due to overgrazing, trampling, and rooting. In the case of beavers, alteration is due to tree cutting for dam construction, which causes large tracts of *Nothofagus* forests to be flooded.

4. THE SPECIES

"Las hayas del hemisferio austral, tenidas por tales hasta el siglo pasado e incluidas en el género *Fagus*, fueron separadas de éste por Blume, para constituir el género *Nothofagus*, que, con este *nothos* griego, nos trae la idea de bastardía."

P.Font Quer (1974).

Origin and diversification

Nothofagus (Gk. *nothos*= false and Gk, L. *phegos, fagus*= beech; "fagus" refers to the nuts) comprises thirty-five tree species (Poole 1987, Hill & Jordan 1993) (table 12). It is possible that the author who described the genus had wanted the name to mean "southern beach", in which case it should have been *Notofagus*, from *notos*= southern (Hyam & Panckhurst 1995). *Nothofagus* was originally part of the family Fagaceae given its undisputed relationships with *Fagus*, *Castanea*, and *Quercus*. However, at present there is an ample consensus to include it within the monogeneric family Nothofagaceae (e.g., Thorne 1983, Jones 1986, Romero 1986, Cronquist 1988, Nixon 1989). This division is primarily justified by the differences in pollen aperture, ovule integument, ontogeny, and in the arrangement of the male inflorescence between *Nothofagus* and the other fagaceous genera. Though similarities in the chloroplast enzymes and in the phloem suggest a close connection between *Nothofagus* and *Fagus* (Hill & Jordan 1993, Martin & Dowd 1993), the presence of a single integument in the ovule, a porous pollen, and a distichous phyllotaxis suggests instead a stronger alliance between *Nothofagus* and *Betula* (Nixon 1989).

Initially, the deciduous and evergreen character was the primary basis for the infrageneric classification of *Nothofagus* in sections, e.g., Calucechinus, deciduous, and Calusparassus, evergreen (van Steenis 1953, 1954, Philipson & Philipson 1988). Nevertheless, recent studies suggest that this habit represents a multiple evolutive convergence, and therefore it is no sufficient criterion for a generic subdivision (Hill & Read 1991). The modern infrageneric taxonomy of the fossil and extant species is based on the size, form, and aperture of the pollen. This element shows a distinctive morphology. It is produced abundantly and is preserved adequately over long periods. Dettmann et al.(1990) recognise eight different pollen types, designated ancestral (a) (represented by *Nothofagidites senectus* of an extensive distribution during the late Cretaceous of southern Gondwana), ancestral (b) (represented by *Nothofagidites endurus* from southeastern Australia and *Nothofagidites kaitangensis* from New Zealand, both occurring in the early Palaeocene), *Nothofagus brassii* (a), (b) and (c), *Nothofagus fusca* (a) and (b), and *Nothofagus menziesii*. Only *Nothofagus brassii* (a), *Nothofagus fusca* (a) and (b), and *Nothofagus menziesii* pollen types are found within the extant species. Following this pollen classification, living southern beeches are arranged in four subgenera (Hill & Read 1991) (table 12).

The first fossil record indubitably belonging to *Nothofagus* is *Nothofagidites senectus*, from the late Cretaceous (85–75 Ma) (Romero 1988, Dettmann et al. 1990). The origin of the group presumably took place during the late Cretaceous in southern South America–Antarctica, in part of the biogeographical Province of Wedell (Dettmann et al. 1990). This province also encompassed Tasmania, southeastern Australia, and New Zealand, which were terrestrially connected during the whole Mesozoic era (Dettmann et al. 1990). Another hypothesis suggests that a Fagales complex, existing in southeastern Asia–Australia, gave rise, on the one hand, to Fagaceae (*s.str.*) and Betulaceae that migrated to the northern hemisphere, and on the other hand, to a group that moved to southern latitudes to give rise there to *Nothofagus* (Hill 1992). Then, the genus diversified and expanded rapidly. Pollen types of extant species come from the late Campanian of the Antarctic peninsula (84 Ma) and the Maastrichtian of South America (75 Ma), a region which constituted the centre of diversification for *Nothofagus* during the late Cretaceous (Dettmann et al. 1990). The later occurrence of extant pollen types in New Zealand and Australia (Palaeocene and Eocene, 66.4–36.6 Ma) would represent a migration route that involved West Antarctica (Dettmann et al. 1990).

The species that produced a *Nothofagus brassii* pollen type, at present confined to New Guinea and New Caledonia (table 12), probably originated in western Antarctica and southern South America. Then, during the Eocene and Oligocene they migrated towards Australia, Tasmania, and New Zealand. At the end of the Tertiary these species became extinct presumably in response to climatic change, although some of them persisted in Tasmania until the Pleistocene (Macphail et al. 1993). In Antarctica, from the end of the Cretaceous to the beginning of the Miocene (66–24 Ma) the terrestrial biota gradually became simpler as the continent migrated to higher southern latitudes. *Nothofagus* constituted the most conspicuous species, exhibiting deciduous, wide leaves during cold periods and persistent, small leaves during warm periods (Hill 1992). The low fruit dispersal capacity and the presence of a specific atmospheric circulation would explain their continuous presence until the Pliocene (5.3 Ma), when the genus became locally extinct. In the Tasmanian sediments from the Oligocene all the extant subgenera of *Nothofagus* coexist. However, at present only Fuscospora and Lophozonia are found there. The tropical Brassospora became absent from other regions probably because of a change towards a more seasonal temperate climate (Read et al. 1990). In Tasmania, the modern absence of Nothofagus and their presence under a similar physical setting in South America is a paleoecological question that at present has no answer (Read et al. 1990). The subgenus Nothofagus represents a continental endemism for South America. *Nothofagus* from this region is characterised by the highest subgeneric richness, and includes *Nothofagus alessandrii*, the most primitive living *Nothofagus* species (Hill & Dettmann 1996) (tables 12, 14).

The monospecific genus *Austrocedrus* (L. *Austro*= southern, Gk. *kedros*= cedar) is part of the conifers, the largest and most diverse group of living gymnosperms. Conifers flourished and dominated terrestrial landscapes for 160 million years during the Mesozoic. They began to decline when angiosperms expanded towards the end of this era. Living conifers are a small remnant of a former more diverse and widely spread group, at present represented by 559 species and 7 families. Extant conifers are either primarily of the northern or of the southern hemisphere, forming two very contrasting groups that diverged during the late Carboniferous and Permian (290 Ma) (Li 1953b, Florin 1963). There are only a very few, exceptional cases in which a conifer groups crossed the tropics. A clear geographic differentiation of taxa is perceived in the occurrence of the southern hemisphere families Podocarpaceae, Araucariaceae, and the cupressaceous subfamily Callitroideae, and of the northern family Pinaceae and the cupressaceous subfamily Cupressoideae. In contrast with the coniferous taxa restricted to the northern hemisphere that tend to dominate the landscape (e.g., *Abies* (Pinaceae), *Picea*, *Pinus*, *Larix*), those from the south often have been regarded as relics and "uncompetitive" trees (Florin 1963). Within a floristic region they tend to have few species per genus or family. The majority of the endemic or disjunct conifers are concentrated in mountainous, moist and warm regions, bordering the eastern and western parts of the Pacific basin (Li 1953b). The disjunct distribution pattern of southern conifers is explained by the effect of continental drift on a common ancestor, which is thought to have inhabited Gondwana. Long–distant dispersal has not been as frequent as in angiosperms, given the relatively large size of most conifer seeds. Since the Miocene (about 24 Ma), both the extinction and the range retraction of conifers occurred in the southern lands, but regional extinction was not global at genus level (Kershaw & McGlone 1995). For instance, *Podocarpus* became extinct in southern Europe and North America, and *Araucaria* in New Zealand, whereas both are still extant in South America.

Austrocedrus chilensis belongs to the most widely spread family of living conifers, since the Cupressaceae exhibits a bihemispheric distribution (table 17). The family comprises around 118 living woody species, of which 36 occur only in the southern hemisphere and only one, *Juniperus*, is

Table 17: Geographical distribution of the 37 species of Cupressaceae from the southern hemisphere (subfamily Callitroideae, *sensu* Li 1953a). The first number indicates the total species richness of the genera, the second between brackets the total number of species within the region. Underlined species are those found in temperate rainforests. The genera *Calocedrus*, *Chamaecyparis*, *Cupressus*, *Fokienia*, *Platycladus*, *Tetraclinis*, *Thuja*, and *Thujopsis* are restricted to the northern hemisphere (subfamily Cupressoideae except *Tetraclinis*, *sensu* Li 1953a).

<table>
<tr><th>Region</th><th colspan="3">Genera and species</th></tr>
<tr><td>Africa
5 spp</td><td colspan="2">*Widdringtonia* 4(4)
W.cedarbergensis, W.cupressoides, W.scwarzii, W.whytei</td><td>*Juniperus* 50(1)
J.excelsa</td></tr>
<tr><td>Australia
18 spp</td><td>*Actinostrobus* 3 (3)
A.acuminatus, A.arenarius, A.pyramidali</td><td>*Callitris* 16 (14)
C.baileyi, C.collumellaris, C.drummondii, C.endlicheri, C.intratropica, C.glaucophylla, C.macleayana, C.monticola, C.muellerii, C.oblonga, C.preissii, C.rhomboidea, C.roei, C.verrucosa</td><td>*Diselma* 1 (1)
D.archeri</td></tr>
<tr><td>New Caledonia
6 spp</td><td>*Callitris* 16(2)
C.neo-caledonica, C.sulcata</td><td>*Libocedrus* 5 (3)
L.austracaledonica, L.chevalieri, L.yateensis</td><td>*Neo-callitropsis* 1(1)
N.pancheri</td></tr>
<tr><td>New Guinea
3 spp</td><td colspan="3">*Papuacedrus* 3 (3)
P.arfakensis, P.papuana, P.toricellensis</td></tr>
<tr><td>New Zealand
2 spp</td><td colspan="3">*Libocedrus* 5 (2)
L.bidwilli, L.plumosa</td></tr>
<tr><td>S.America
3 spp</td><td>*Austrocedrus* 1 (1) *A.chilensis*</td><td>*Fitzroya* 1 (1)
F.cupressoides</td><td>*Pilgerodendron* 1 (1) *P.uviferum*</td></tr>
</table>

localised in both hemispheres (table 17). In view of the phylogenetic affinities, Eckenwalder (1976) and Miller (1988) have proposed a merger between Cupressaceae and Taxodiaceae, a small family with only the genus *Athrotaxis* occupying the southern hemisphere within Tasmania. There is a clear phylogenetic separation between the northern (subfamily Cupressoideae) and the southern Cupressaceae (subfamily Callitroideae), both forming a monophyletic group (Gadek & Quinn 1993). Cupressaceae is regarded as a relictual group as many extant genera are monotypic (such is the case of *Austrocedrus* and other four southern genera). They also may include few species, each with a very limited geographic distribution (table 17). Cupressaceae is a very ancient plant group as it was in existence by the early Mesozoic, but it is unknown when it originated. Although their fossils are abundant and widespread in the Mesozoic and Tertiary sediments, their taxonomic position remains doubtful (Eckenwalder 1976). Nearly all the earlier Mesozoic fossils assigned to this taxon belong to one extinct family (Miller 1988). The oldest fossils assigned to this family have been found in several sediment deposits of the late Triassic and late Cretaceous from France, Israel, and North America (about 200–70 Ma) (Hill 1995). Fossil twigs, leaves, cones, and wood still found in modern groups (e.g., *Widdringtonia*, *Callitris*) have been recognised in records since the early Cretaceous (about 140 Ma) (Miller 1977).

The cladogram constructed by Hart (1987) strongly suggests that the cupressaceous genera restricted to the southern hemisphere originated in Gondwana (table 17, except *Juniperus*). The evolutive history of southern coniferous taxa has been poorly studied. Their Quaternary history is based almost entirely on palynological analysis because pollen can be well recognised within the group, and because macrofossil records are almost absent (Kershaw & McGlone 1995). Southern Cupressaceae are much less widely spread and less diverse at species level than the northern group. Their source of macrofossils is centred in south–eastern Australia, where *Austrocedrus*, *Callitris*, *Libocedrus*, *Papuacedrus*, and *Athrotaxis* were found. The oldest record is an undescribed species of *Libocedrus* from the late Palaeocene and early Eocene of southern mainland Australia and Tasmania (50 Ma) (Hill 1995). The closely related *Austrocedrus*, *Libocedrus*, and *Papuacedrus* (*Libocedrus*–pollen type) have been found in Oligocene – Miocene sediments from northern Tasmania (36–10 Ma) (Hill & Carpenter 1989, *ex* Hill 1995). The fact that the morphological differences among them were as pronounced as today, and that *Papuacedrus* and *Libocedrus* were found in a single deposit in northeastern Tasmania, suggests an even older evolutionary history of the group (Hill 1995). *Libocedrus*–type macrofossils have been also recovered from Tertiary sediments of the Antarctic peninsula, South America, and New Zealand, but their significance is not yet clear (Hill 1995). Florin (1963) described some macrofossils from the Eocene of South America (58 Ma) as morphologically identical to *Austrocedrus chilensis*, which indicated its long evolutive history inside the present distribution. Eckenwalder (1976) proposed that *Austrocedrus* and the members of the family confined to the south could have originated from a *Cupressus*–like ancestor. Florin (1963) suggested that a probable migration route involved New Zealand, Antarctica, and South America, during the Mesozoic and early Tertiary.

Biology and distribution

Nothofagus is composed of prominent and dominant trees confined to tropical and temperate areas of the southern hemisphere, in New Guinea, New Caledonia, New Zealand, southern and eastern mainland Australia, Tasmania, and southern Chile and Argentina (table 17). They exhibit an evergreen or deciduous habit, with simple, alternate, distichous leaves with a cartaceous or coriaceous texture. The genus shows a dicliny–monoecious breeding system, with male and female flowers in the same individual. Nevertheless the deciduous species manifest both an asexual and a sexual mechanism of propagation, the latter is far more important in terms of habitat colonisation and persistence. Trees are supposed to be self–incompatible, which may favour cross–fertilization (Allen & Platt 1990). Male flowers are axial, solitary or grouped in 2 to 3 conforming an inflorescence. Up to seven female flowers are inserted at the base of a cupule or perianth composed of a short peduncle and 2 to 6 valves. The pollen grain is adapted to anemophilic pollination. Seeds are exalbuminous with epigeous germination. The fruit is a dimerous or trimerous one–seeded achene (nut), more or less distinctly winged and encompassed by an involucrum with appendages. In South American *Nothofagus*, the fruit consists of a central mass and 2 to 3 wings depending on the species. Particular morphological properties of *Nothofagus dombeyi* are shown in table 14.

In South America, from 32° to 55°30'S, four deciduous *Nothofagus* species with large leaves, two deciduous ones with small leaves, and three evergreen species with small leaves are present. There are also several natural hybrids such as *Nothofagus leonii* = *Nothofagus obliqua* x *Nothofagus glauca*, and varieties such as *Nothofagus obliqua* var. *macrocarpa* (Donoso & Landrum 1979) (table 14). The deciduous habit is almost exclusively found within this region: six out of nine *Nothofagus* are deciduous, whereas at a global scale only seven out of thirty–five are deciduous. All the nine South American species of *Nothofagus* naturally occur in Chile, six of them are localised in Argentina as well (table 14). Both *Nothofagus pumilio* and *Nothofagus antarctica*, and *Nothofagus alessandrii* exhibit the largest and the smallest geographical distribution, respectively. *Nothofagus glauca* determines the northern geographical limits of the genus, while *Nothofagus betuloides* and *Nothofagus pumilio* the southern limits (table 14). *Nothofagus glauca* exhibits a fruit that is around 300 times heavier than those of the other *Nothofagus* species from South America (table 14). All the evergreen species (*Nothofagus dombeyi, Nothofagus betuloides,* and *Nothofagus nitida*) reproduce exclusively by seeds (table 14).

Nothofagus dombeyi is one of the largest trees in the biome, reaching a maximum height of about 50m and a diameter of more than 2m. It spreads at both sides of the Andes from 35° to 47°30'S at altitudes up to 1,300m, on well–drained sites with annual precipitation varying from 1,400 to 5,000mm (Dimitri 1972). *Nothofagus dombeyi* forms monospecific forests on perhumid and warm sites in the northern part of its geographical range, whereas in the southern part it is confined to sites showing intermediates heat and humidity (Ramírez et al. 1988). In Chile, at low and mid–elevations *Nothofagus dombeyi* usually constitutes the emergent and upper stratum of the virgin Valdivian forests. Here, a dense matrix of several shade–tolerant, broadleaved and coniferous trees is present in the intermediate layer, with an understorey occupied by various bamboos of the genus *Chusquea*. The northernmost limit of this species is located around 34°S, where the trees forms stands mixed with the deciduous *Nothofagus glauca* in areas with high moisture content, such as valley bottoms or the shores of rivers and lakes (San Martín & Donoso 1995). In the rain shadow of northern Patagonia, Argentina, in the more humid sites it mostly occurs in monospecific stands. Towards the east it becomes mainly associated with the more drought–tolerant *Austrocedrus chilensis* and *Nothofagus antarctica*, two species that extend farther east surrounded by the steppe. Towards the south, *Nothofagus dombeyi* is replaced by the evergreen *Nothofagus betuloides* at around 47°S.

Austrocedrus chilensis is an inherently long–lived conifer, of which individuals older than 1,000 years have been found (LaMarche et al. 1979). However, these are very exceptional cases given the frequent occurrence of episodes of stand mortality caused by massive allogenic impacts. Often, in old–growth stands, trees are estimated to live for 500 years (Enright & Odgen 1995). This species shows one of the widest ecological amplitudes in South America, reflecting its capacity to withstand the xeric conditions occurring in the northern and the eastern limits of the biome. In Argentina, *Austrocedrus chilensis* extends in a narrow fringe from 36°30' to 43°35'S (Seibert 1982), reaching a maximum altitude at 1,100m, and covering around 1,600km^2 (Dezzotti & Sancholuz 1991) (figure 6). Within the rain shadow of northwestern Patagonia, this species is present as a dominant or subdominant tree along the transition from the temperate *Nothofagus*–dominated forest in the west, to the dry steppe in the east (figures 6, 7). At 40°S, in the drier areas (600–900mm annual precipitation) *Austrocedrus chilensis* forms pure and sparse woodlands mostly on elevated, more humid sites surrounded by the steppe, exhibiting low tree biomass, density, and growth. In western areas of intermediate rainfall (900–1,400mm), it develops pure, dense forests attaining the highest values of abundance and productivity recorded for the species. In the more humid zones towards the west (1,400–1,800mm), it becomes a subdominant trees underneath the emergent and dominant layer of *Nothofagus dombeyi* trees. In Chile, this species shows a wider latitudinal and altitudinal distribution ranging from 32°39' to 44°S, and up to 1,800m (Hueck 1978). However, the actual area covered by the species is relatively low (Donoso 1993). *Austrocedrus chilensis* constitutes associations with the sclerophyllous woody plants within the Mediterranean–type of climate of central Chile, such as *Quillaja saponaria* (Rosaceae) and *Lithrea caustica* (Anacardiaceae). In more humid sites, this species forms mixed communities with *Nothofagus obliqua* and *Nothofagus glauca*.

In the drier sites, multi–stemmed, low individuals within expanded crowns are common. Under more humid conditions, the species adopts a pyramidal shape attaining more than 35m height. It possesses decussate, coriaceous, scale–like, weakly cutinised leaves, markedly dimorphic with facial and marginal types differing in size and form. In Argentina, *Austrocedrus chilensis* exhibits primarily a dioecious conservative character: individuals are either males or females along the whole life cycle as shown in an extensive study (Brión et al. 1993). In Chile, this species is frequently described in literature as a dicliny–monoecious plant (Hoffmann 1982, Serra et al. 1985, Donoso 1993), although experimental studies to support this claimed breeding system have not been specifically carried out there. Its main mechanism of reproduction is sexual, although vegetative propagation from basal sprouts may occurs in very dry sites (pers. orbs., Le–Quesne 1988). Male strobili are spherical and 1 to 4mm long while female cones are 10 to 15mm long, exhibiting 4 valvate scales each having a minute tubercle at the back. "Flowering" occurs from September to November. Seeds are 3 to 5mm long, with two single, lateral wings, one of them rudimentary.

Species and forest dynamics

In the *Nothofagus* species from South America, the development of a new cohort of propagules is completed along a 4–year reproductive cycle. Floral primordia are formed from September (first year) and become dormant at the beginning of the cold season. Flowering begins the next September (second year), pollination and fructification extend until February (third year), and seed dispersion occurs between March and April (third year). Germination takes place between October and February (fourth year), after seeds have passed the cold season as dormant in the soil. Seed production is a discontinuous and irregular process as observed in many other forest tree species (Harper 1977, Poole 1987), as there are “mast years” with abundant seed crop alternating with

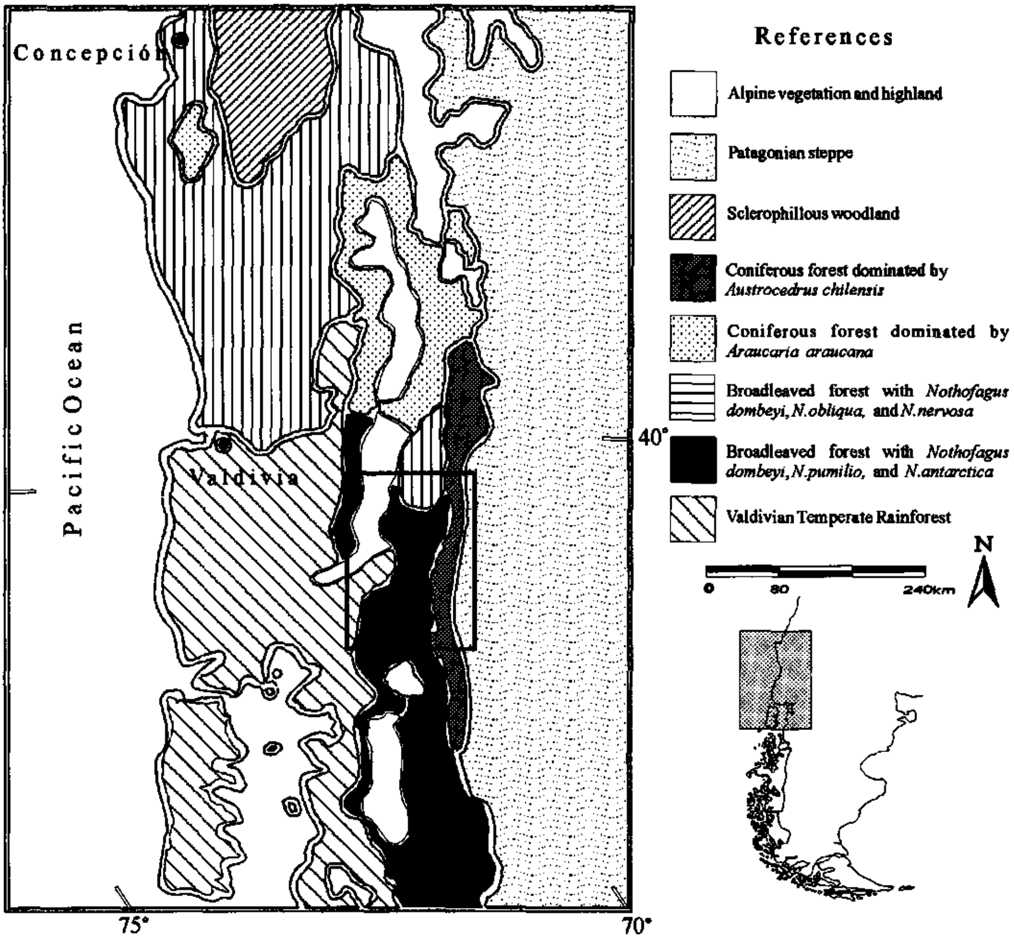
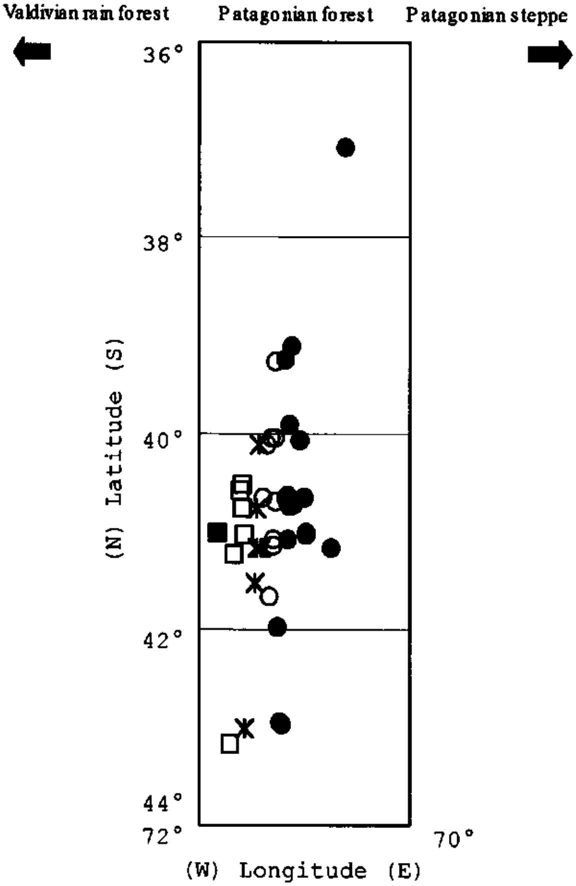


Figure 6: Geographic distribution of the main vegetation types localised in the southern Andes between 33° and 43° S. (Hueck 1978, Donoso 1993). The frame indicates the area depicted in figures 10 and 29.

periods of very scarce seed crops (Burschel et al. 1976, Murúa & González 1985, Donoso et al. 1993). Periodic heavy seeding is related to a number of environmental and endogenous factors, interacting over the long period between initiation of flower buds and dispersal of fruits (Allen & Platt 1990). Viability of recently dispersed seeds is proportionally low, and increases during mast years (Burschel et al. 1976, Donoso et al. 1993, Muñoz 1993). Seeds are frequently not fertilised or predated, as their edibility made them a ready food for frugivores. In *Nothofagus* seeds, pre–dispersal predation by microlepidoptera of the genus *Perzelia* and post–dispersal predation by rodents reached 62% and 70%, respectively (Cruz 1981, *ex* Bustamante 1995, Bustamante 1995). Seeds and seedlings, particularly those from *Nothofagus dombeyi*, are very cold and dry–resistant, which is interpreted as an adaptation to the extremes in heat and humidity in many environments (Alberdi 1995).

Figure 7: Location of several pure and mixed stands in northwestern Patagonia, Argentina. *Austrocedrus chilensis* woodlands (filled circles), *Austrocedrus chilensis* forests (empty circles), *Austrocedrus chilensis* - *Nothofagus dombeyi* forests (asterisks), *Nothofagus dombeyi* forests (empty squares), and temperate rainforests (filled squares), are represented.

Sources: Pita (1931), Frangi (1976), McQueen (1976, 1977), LaMarche et al. (1979), Dezzotti & Sancholuz (1991), Anonymous (1994), Kitzberger et al.(1995), Lucero (1996), Villalba & Veblen (1997a,b). At 41° latitude, the distance between two grades of longitude equals 84km.



South American *Nothofagus* species are light–demanding, as shown in many ecophysiological and ecological studies (Hueck 1978, Gutiérrez et al. 1991, Rush 1992, Veblen 1992, Rebertus & Veblen 1993). However, important differences in light response have been found amongst species and development stages (figure 8). Although the species require a high light intensity, early phases of development are particularly sensitive to the heat occasioned by strong radiation, and the consequent drought. For instance, in nursery and plantations juveniles of *Nothofagus dombeyi*, *Nothofagus nervosa*, and *Nothofagus obliqua* exhibited a larger size and biomass and a lower mortality under an intermediate light regime than under a very open or closed condition (Aguilera & Fehlandt 1981, Müller–Using & Schlegel 1981, Grosse & Bourke 1988). In *Nothofagus* plantations, Grosse (1988a) reported a total and a 50% sapling mortality under a completely open and closed canopy, respectively, whereas at an intermediate luminosity survival comprised more than 90% of the original cohort.

Judging by its performance under different light treatments, *Nothofagus dombeyi* appears to require more light in comparison not only with the other *Nothofagus*, but also with other dominant, co–occurring species (Espinosa 1972, Rosenfeld 1972, Read & Hill 1985). In a comparative trial, Grosse (1988b) found that *Nothofagus dombeyi* required at least 3.9% relative luminosity (RL) for seedling survival, whereas *Nothofagus obliqua* and *Nothofagus nervosa* demanded 2.2% and 3.1% RL,

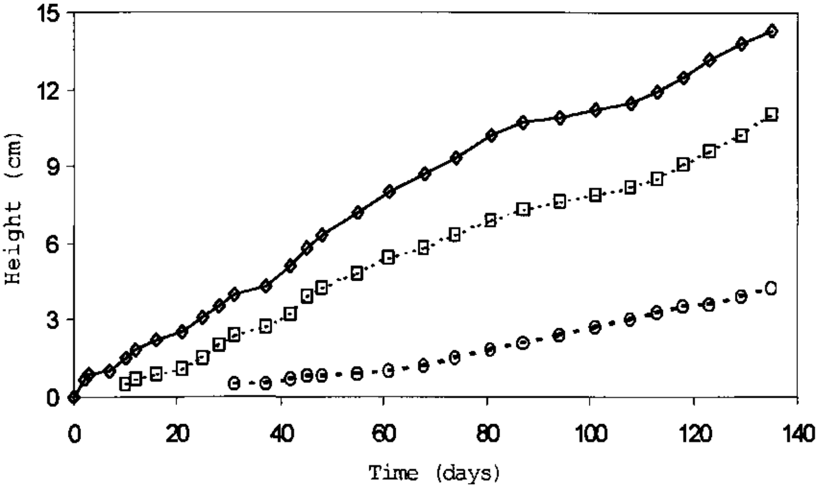


Figure 8: Height growth of *Nothofagus nervosa* (continuous line, triangles), *Nothofagus obliqua* (dashed line, squares), and *Nothofagus pumilio* seedling (dotted line, circles), during the first growing season under an intermediate light intensity regime (data from Guerra 1986).

respectively. Responses of juveniles to light in these co–occurring *Nothofagus* species have been also exhaustively analysed by Müller–Using & Schlegel (1981). They carried out a nursery experimentation over 2 years, in which soil water content was maintained continually at optimum level to avoid the dehydrating effects associated to high radiation. During the first growing season, *Nothofagus dombeyi* experimented a lower development in comparison than any of the other congenerics, regardless of light intensity. However, at the end of the second period *Nothofagus dombeyi* reached the greatest size under the highest luminosity (figure 9). The enhanced early development of the species with large seeds *Nothofagus nervosa* and *Nothofagus obliqua* is convincingly explained by the reserves stored in the propagule. *Nothofagus dombeyi* would have undergone physiological constraints during establishment, given its small seeds. However, once it overcame this critical periods it showed an enhanced performance. *Nothofagus dombeyi* passes over the other tree species, particularly under an intermediate and high light regime (Müller–Using & Schlegel 1981). Seed size and initial growth performance are well balanced against each other, as found in many tree species (Crawley 1997a). Differential responses of juveniles to light may represent a mechanism by which *Nothofagus* species are able to co–exist in compositional equilibrium, characterised by the absence of successional replacement of species. Co–occurring *Nothofagus* species certainly have evolved in contrasting "regeneration niches" (*sensu* Grubb 1977), particularly in terms of light requirements, so avoiding any direct interference while at the same time using the available resources optimally for keeping alive.

The ecology of *Nothofagus* regeneration has been examined by McQueen (1976, 1977), Veblen & Ashton (1978), Veblen et al.(1979, 1980, 1981), Veblen (1982, 1989), Veblen & Lorenz (1987), Armesto & Figueroa (1987), Armesto & Fuentes (1988), Gutiérrez et al.(1991), Innes (1992), Rush (1992), Donoso (1993), and Rebertus & Veblen (1993) (table 18). *Nothofagus* dynamics are influenced by i) the heliophilous, rather light–demanding, opportunistic character of their species, ii) the capacity to endure harsher conditions than most of its neighbouring species (Wardle 1983), and iii) a spatially changing environment due to a particular regime of impacts, which exerts important influences on the performance of associated trees and understorey species (Veblen 1989). *Nothofagus* primarily exhibits a "catastrophic regeneration mode" (*sensu* Veblen 1992) or a "seedling regeneration mechanism" (*sensu* Bazzaz 1983) (table 19). It rapidly colonises open sites forming even–aged populations following the synchronous elimination of previous vegetation, caused by the periodical occurrence of large–scale (>2,500m^2), allogenic impacts (earthquakes, volcanism, landslides, fires, windstorm). In absence of such heavy impacts, more shade–tolerant, late successional species such as the broadleaved *Aextoxicon punctatum*, *Laureliopsis philippiana*, and *Persea lingue*, and the conifers *Saxegothaea conspicua* and *Podocarpus nuvigena*, become continuously established in the understorey (table 18).

After some 150 years, the advance regeneration of the primary species occupies fine–scale gaps (e.g., <1,000m^2), reaching maturity and forming uneven–aged populations. As long as the forest development continues, these species are expected to successionally replace *Nothofagus*. Southern beeches are not able to become established underneath the main canopy or in small, autogenic gaps, given the low light levels and the density of shade–tolerant plants in the undergrowth. However, the heavy intensity and high frequency, as compared with *Nothofagus* longevity, of the impact regime associated to the mountainous areas, throws the slow population dynamics off course and provides the ecological conditions for new establishment of *Nothofagus* seedlings, so preventing the development of vegetation lacking *Nothofagus*. The major effect of the impact regime is to interrupt any directional change in community composition, and to maintain forests in an early stage of development.

The above explains the dynamic of *Nothofagus* forests located in the non–seasonal, floristically more diverse lowland sites of the Valdivian district, where two significant conditions occur: the existence of shade–tolerant species able to substitute *Nothofagus*, and the persistence of allogenic large–scale impacts (Veblen & Ashton 1978, Veblen et al. 1979, 1980, 1981). However, in many lowland areas to the west to the Andes, there are large tracts of coastal mixed broadleaved rainforests mainly dominated by shade–tolerant myrtaceous trees and *Laureliopsis philippiana*, from which *Nothofagus* is frequently absent. These communities are interpreted as representing advanced stages of forest development, in compositionally equilibrium as opposed to the process of successional replacement observed in Andean forests (Donoso et al. 1985, Armesto & Figueroa 1987, Armesto & Fuentes 1988, Lusk 1996). Given the higher distance to the tectonically active Andes, coastal areas are much less susceptible to heavy impacts causing permanent dominance of *Nothofagus*. Here, trees dominant in the canopy continuously establish seedlings in the understorey or in small–size gaps due to autogenic events. Toward the south and east, in suboptimal sites and at higher elevations, the biome becomes progressively poorer in tree species, especially in the more shade–tolerant ones. As a result of the absence of shade–bearer trees, neither successional replacement of *Nothofagus*, nor change in species composition are likely to occur (Veblen 1989, Rebertus & Veblen 1993). Understorey replenishment may start with *Nothofagus* seedlings after 150–200 years, when medium–sized light–gaps of 250–500m^2 are opened up by the fall of senescent old–growth *Nothofagus* (Veblen et al. 1981). A "gap–phase regeneration mode" within small light openings (*sensu* Veblen 1992) is also observed in *Nothofagus dombeyi* and other southern beeches such as *Nothofagus nitida*, in stands lacking shade–tolerant trees (Innes 1992).

Table 18: Patterns and processes of mature *N.dombeyi* and *A.chilensis* forests in Patagonia.

Location	Forest District [1]	Forest dynamics	Rainfall (mm yr^{-1})	Allogenic impact	Forest structure and composition					Regenerative ecology [6]
					Physiognomy	Dominant	Composition [3]	Shade-tolerant [4]	*Chusquea*	
Western Andes (Chile)	Valdivian Rainforest	Successional replacement	2,000–4,000	Geological and climatic [2]	Highly mixed, closed, multi-layered, evergreen, broadleaved, conifer, closed understorey, high diversity of life-forms.	*D.winteri*, *S.conspicua*, *P.lingue*, *L.philippiana*, *E.cordifolia*		Present	*C.culeou*, *C.quina*	Coarse-scale, stand-devastating disturbances are particularly relevant in vegetation dynamics. Following such events, *Nothofagus dombeyi* colonises sites by forming even-aged populations. During understory reinitiating stage, through advance regeneration shade-tolerant trees pre-empt fine-scale gaps which become important during forest development. Proliferation of *Chusquea* beneath the canopy together with the thick accumulation of its litter also prevents *N.dombeyi* regeneration. Periodic major impacts disrupt the processes of long-term interaction and fast population dynamics, promoting the persistence of *N.dombeyi*-dominated forests.
Eastern Andes (Argentina) [5]	Patagonian rainforest	Species coexistence and compositional equilibrium	1,600–2,000		Pure, closed, single-layered, evergreen, broadleaved, closed understorey.	*N.dombeyi*	*S.patagonicus*, *L.hirsuta*, *M.boaria*, *E.coccineum*	Absent	*C.culeou*	*Nothofagus dombeyi* establishes in sites after the occurrence of massive impacts, but these events are not essential for the continued dominance of this light-demanding species. During forest maturation, light gaps are filled by the vegetative proliferation of the clump-forming *Chusquea* bamboo that interferes critically with tree recruitment (low light-levels and competition for other resources). However, *N.dombeyi* regeneration re-occupies the site after the gregarious flowering and die-off of *Chusquea* populations occurring at intervals larger than one year.
			1,400–1,800	Forest fire	Two-species, closed, double-layered, evergreen, broadleaved-conifer, open understory.	*N.dombeyi*–*A.chilensis*				Long-term co-occurrence of the two dominant tree species *Austrocedrus chilensis* and *Nothofagus dombeyi* is probably based in resource partitioning or niche differentiation, so that these species coexist without competing directly. The successful recruitment of tree species in both treefall and large gaps, is favour by the absence of both the inhibitory influences of shade-tolerant canopy-dominant tree species, and the *Chusquea* species.
			600–1,400		Pure, open/very open, single-layered, evergreen, conifer, low stature, open understory.	*A.chilensis*			—	*Austrocedrus chilensis*- dominated stands constitute stable communities, exhibiting self-replacing processes after both coarse-scale and small-scale disturbances.

(1) According to Veblen et al.(1983). (2) It comprises earthquake-triggered landslides, glacial movement, deposition of volcanic ash and flood, and blowdown. (3) See table 11 for further references. (4) It particularly refers to potentially dominant canopy tree species. (5) The Valdivian rain forest district also occurs in Argentina in very small areas. (6) Following Burschel et al.1976, Veblen 1982, Veblen & Ashton 1978; Veblen et al.1981, Donoso et al.1984,1985, Armesto & Figueroa 1987, Veblen & Lorenz 1987, 1988, Armesto & Fuentes 1988.

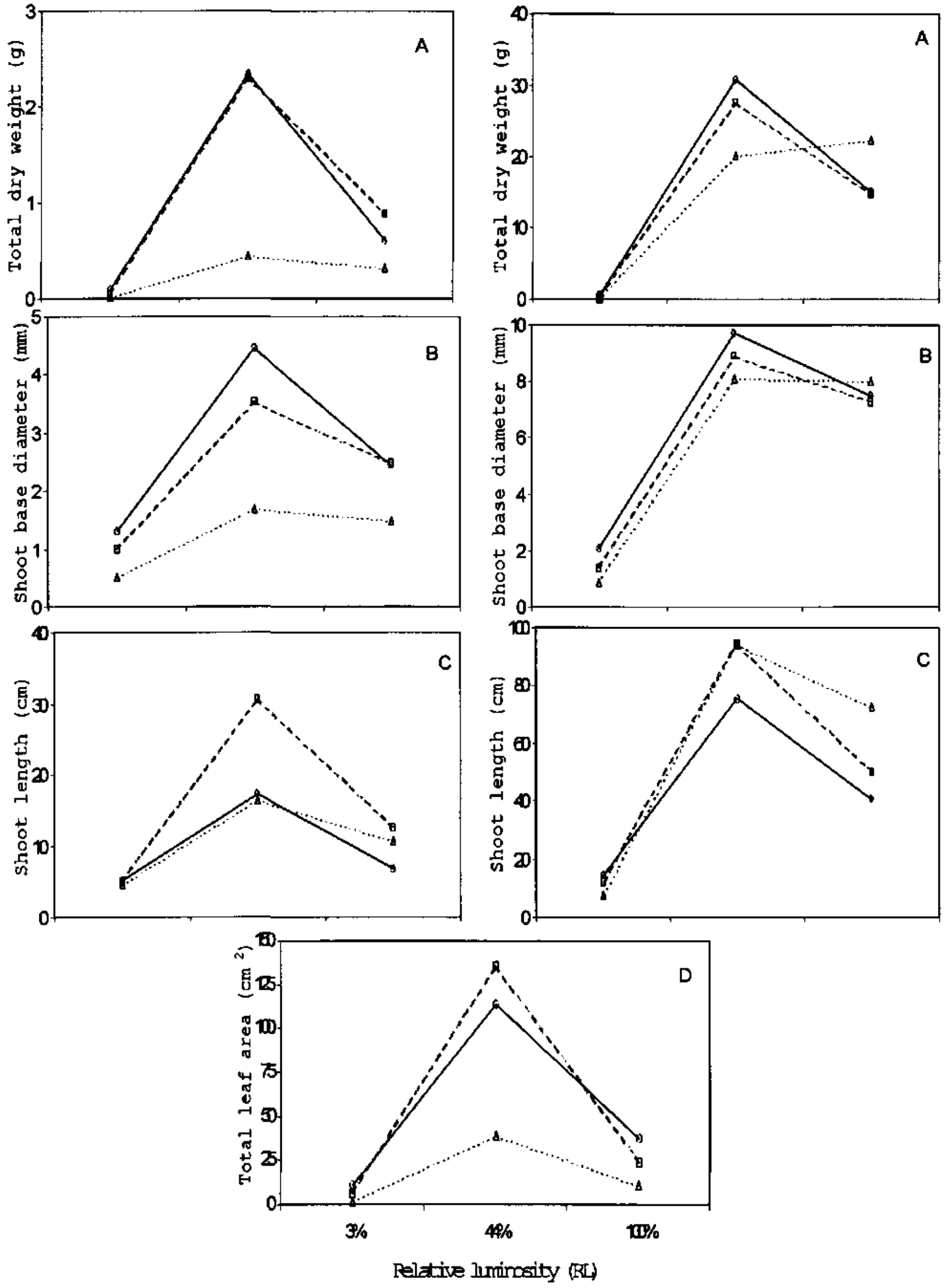


Figure 9: Total dry weight (A), root collar diameter (B), total height (C), and leaf area (D) of *Nothofagus dombeyi* (triangles, dotted line), *Nothofagus nervosa* (circles, continuous line), and *Nothofagus obliqua* (squares, dashed line) seedlings, under three light regimes after the first (left) and the second vegetative growth period (right) (data from Müller-Using & Schlegel 1981).

Table 19: Establishment of plants in response to the scale, severity, and duration of ecological impacts (Bazzaz 1983, Peterken 1996). A: absent, C: common, P: predominant, and O: occasional.

Impacts	Reaction				
	Asexual		Sexual		
	Expansion	Sprouting	Advanced regeneration	Seed bank	Immigrant
Mild, not prolonged, very small canopy openings (windthrow, glaze storms)	P	A	C	A	A
Mild, large canopy openings (blowdowns)	O	C	C	C	C
Severe, not prolonged (fires)	A	C	A	P	C
Very severe, not prolonged (landslides, vulcanism)	A	O	A	O	P
Very severe, prolonged (agriculture)	A	A	A	A	P

In the low– and mid–elevation stands of the subantarctic forests, colonisation and early development of *Nothofagus* is impaired by the massive proliferation of *Chusquea*. This is an indigenous bamboo genus occurring in Central and South America. In Argentina, the most widely spread species is the monocarpic *Chusquea culeou*. It forms dense thickets particularly in rather humid, virgin stands along the eastern Andean slopes from 35° to 45°S, and at elevations up to 1,400m. The bamboo forms clonal clumped populations with a large biomass, in the open as well as beneath a dense *Nothofagus* canopy, by extensive subterranean branching and vegetative propagation according to McClure's model (Hallé et al. 1978). It causes very low light and nutrient levels in the understorey and so inhibits the establishment of the light–demanding *Nothofagus* species, particularly *Nothofagus dombeyi* (Veblen 1982). Bamboo rhizomes and roots form a complex mat within the upper soil horizons. Culms may attain heights of more than 7m (Pearson et al. 1994). Vegetative and reproductive cycles of the bamboos are incompletely known. Some populations have shown intervals of 15 to 25 years between consecutive mass flowerings (Gunckel 1948), while in other regions synchronic blooms covering large areas were reported to be farther apart than 50 years (Pearson et al. 1994). Several sporadic blooms over smaller areas were observed, with few plants flowering and dying each year (Pearson et al. 1994). Individuals simultaneously die after flowering, a process that exerts a substantial impact on vegetational succession (Gunckel 1948, Veblen 1982, Pearson et al. 1994). Except for periods of gregarious blooming, flowering bamboos rarely produce seeds, and seedlings are not found directly under parent plants. In Argentina, new and open sites are primarily colonised by seeds mainly dispersed by rodents, rather than by aggressive vegetative growth (Pearson et al. 1994). However, in Chile *Chusquea culeou* is described as an aggressive invader (Veblen 1982). In a dense thicket, 150,000–200,000 culms per hectare were reported (Veblen 1982). There are two main ecological mechanisms which explain the persistence of a recurrent stand structure conformed by a *Nothofagus* overstorey and a *Chusquea* understorey. A first mechanism is driven by environmental impacts: after a large–scale impact, site invasion by bamboo is rapid only if carried out by re–development of surviving rhizomes. If vegetation cover is eliminated completely, fast colonisation by seeds of the arborescent species is more likely (Veblen et al. 1980, Veblen 1982, Donoso 1993). A second mechanism involves the autoecology of the bamboo: the re–development of *Chusquea* populations by seeds, following mass flowering and synchronous death, is a slow process and therefore *Nothofagus* seedlings tend to occupy the sites first (Veblen et al. 1980, Veblen 1982).

In *Austrocedrus chilensis*, seed maturation extends to May (Krebs 1959). Seeds are dispersed by wind, which takes place from April to October. A great proportion of the seeds falls in winter (Lucero 1996). There are large variations in seed production and viability between sites and years (Lucero 1996). In pure stands on optimal sites, seed production and viability are highest, whereas in xeric stands surrounded by the steppe ecotone, records them to be lowest (Sancholuz et al. unpubl.). Seeds are intensely predated by insect larvae, which can consume more than 90% of the total production during some years (Lucero 1996). The size of the soil seed bank varies between 1 and 10% of the total seed production (Sancholuz et al. unpubl.). Seedlings show 2 linear cotyledons. In *Austrocedrus chilensis*, germination and establishment commonly fails in both xeric and mesic sites. In drier areas, sporadic establishment is supposed to respond to a low water content of the soil, and to the desiccating effect of wind and radiation (Costantino 1958, Rovere 1991). At the end of the first year of development, mortality may reach 30% of the original cohort; this process is associated to the effects of both dryness during the growing season and winter cold (Donoso et al. 1986, Lucero 1996). *Austrocedrus chilensis* is little tolerant to shade as reflected by the normal frequency distribution of ages found in their populations (Veblen & Lorenz 1987).

Studies aimed to address the dynamics of *Austrocedrus chilensis* are mostly based on the analysis of population size structure. This approach has marked shortcomings, given the usual lack of correlation between age and diameter of trees. This is observed in plants capable of surviving long periods in extreme sites or under strong suppression, lacking all growth. Stand history analyses based on examination of age structures are rather limited, and mainly focused on stands located in northwestern Patagonia from Argentina (table 18). The dynamics of *Austrocedrus chilensis* are mainly influenced by i) its relatively low shade–tolerance, ii) the pattern of the impact regime, and iii) the extreme variation in site conditions along its geographic range. This last factor is a direct result of the occurrence of the steppe (east) / rainforest (west) ecotone of orographic origin, which determines a divergent composition and abundance of co–occurring species. In more xeric sites towards the east, the physical environment characterised by a high evaporative demand of the air, low rainfall, strong wind, and infertile and shallow soils severly limits forest regeneration, aggravated by recurrent low seed crops (Lucero 1996). The recurrent discontinuous even–aged populations reflect an irregular regeneration, probably depending on periods of favourable conditions (Veblen & Lorenz 1988, Villalba & Veblen 1997a). Intense grazing by domestic cattle and introduced wild herbivores, particularly hares and deer, limits and reduces recruitment (Lebedeff 1942, Veblen et al. 1989b,1992b, Relva & Veblen in press).

In more mesic sites towards the west, *Austrocedrus chilensis* primarily follows a "catastrophic regeneration mode" (*sensu* Veblen 1992), and so forms dense, even–aged, single cohort stands. They develop after the devastation of the original vegetation by large–scale environmental impacts. The most frequent one associated to the mesic stands is fire, to which this species is particularly sensitive given its thin bark. Intense tree shaking and landslides associated to earthquakes also triggers massive mortality in *Austrocedrus chilensis* forests (Kitzberger et al. 1995). In northwestern Patagonia the majority of the post–fire, mesic stands are aged between 70–120 years. They originated from the cessation of the extensive forest burnings caused by white settlers between 1880 and 1930. In mesic areas, secondary succession after fire begins with the rapid colonisation and establishment of propagules, dispersed by wind from adjacent sources or by seeds of occasional surviving trees. Recruitment continues for 50 to 60 years, after which it ceases, probably in response to increase of shade (Veblen & Lorenz 1987, 1988). In several stands, multi–modal age frequency distributions are also found, supposed to occur as a result of regeneration pulses following less intense, not massive fires (Veblen et al. 1992). There are also stands that originated earlier, following fires due either to aboriginals or to natural factors. In these very infrequent, old–growth, mesic forests "gap–phase regeneration" tends to be irregular, given the incapacity of this species for persistence in microenvironments poor in light.

5. THE *AUSTROCEDRUS – NOTHOFAGUS* STAND

> "The differences between trees of the same kind have already been considered. Now all grow fairer and are more vigorous in their proper positions; for wild, no less than cultivated trees, have each their own positions: some love wet and marshy ground, as black poplar, abele, willow and in general those that grow along rivers; some love exposed and sunny positions; some prefer a shady place. The fir is fairest and tallest in a sunny position, and does not grow at all in a shady one; the silver-fir on the contrary is fairest in a shady place, and not so vigorous in a sunny one."
>
> Theophrastus (ca.300 BC).

The present chapter in the synthesis of six articles which were published elsewhere (Dezzotti 1995, 1996a,b, 1999, Dezzotti & Oldeman 1994, Dezzotti & Sancholuz 1995). Because of the synthetic nature of this chapter, the original sharp distinction of introduction, methods, results, and conclusion was lost in part. The reader is referred to the original text.

Methodology

Size and age structures

An experimental area, representative of the intact, natural *Austrocedrus chilensis–Nothofagus dombeyi* association, was chosen for sampling. The criteria for a representative area were the following: it has to show no evidence of major human influences within the life–span of the forest such as logging, agricultural use, burning, plantations, overgrazing, or extensive presence of exotic flora. In order to infer the actions of biotic and abiotic forces to which current trees and their ancestors have been exposed in the past, the size, age and spatial population structures were analysed. Two closely located, permanent square sample plots of 2,500m^2 each were established for intensive sampling (plots A and B). For this analysis, living trees (i) of the two stand–dominant species were categorised as (standard symbols of forest mensuration are according to IUFRO 1956 (*ex* IUFRO 1986, Pardé & Bouchon 1988)):

adults:	$d_{rc} \geq 10$cm,
saplings:	$d_{rc} < 10$cm, $h \geq 50$cm,
seedlings:	$d_{rc} < 10$cm, $h < 50$cm, and
cotyledonary seedlings:	seedlings with embryonic leaves.

in which:

d_{rc} = root collar diameter (cm), and
h = total height (m).

In the plots, each standing adult tree was tagged with a numbered label and measured for d_{rc}

(recorded to the nearest millimetre) with a plastic measuring tape. h (recorded to the nearest centimetre) was indirectly measured using a clinometer, recording angles to the base (α) and to the top of the tree (β), and the horizontal distance from the observer to the tree (l in m, recorded to the nearest centimetre). This observation point was selected in the way that the angle of sight lied between 30° and 45°, as a compromise between the easiest detection of the highest point in the crown and the decreasing of the inaccuracy given the non–linearity relation between tree height and angle of sight. Then, the following equation was used:

$$h = l\,(\tan\alpha + \tan\beta) \qquad (5.1)$$

h of curved trees was estimated by the following empirical functions ($h = F\,(d_{rc})$, $P<0.05$), developed from the remaining database:

for *Nothofagus dombeyi*: $\log_{10} h = 0.084 + 0.733 \log_{10} d_{rc}$ ($R^2 = 0.919$, $N = 40$) (5.2)

for *Austrocedrus chilensis*: $\log_{10} h = 0.363 + 0.559 \log_{10} d_{rc}$ ($R^2 = 0.528$, $N = 138$) (5.3)

Basal area of individual trees (cross–sectional stem area at ground level) (g_{rc}, in m^2) was assumed to be equivalent to that of a circle with the same circumference of the tree. g_{rc} and total individual stemwood volume (v, in m^3) were estimated per tree using the following equations:

$$g_{rc} = 2.5 * 10^{-5}\,\pi\, d_{rc}^{\;2} \qquad (5.4)$$

$$v = g_{rc}\, h f \qquad (5.5)$$

The absolute form factor (f) of *Nothofagus dombeyi* was obtained from an unpublished report of the Universidad Nacional del Comahue. f of *Austrocedrus chilensis* was estimated by the following regression equation ($f = F\,(d_{rc})$, $P<0.05$) (Dezzotti & Sancholuz 1991):

$$f = 0.535 - 2.639 * 10^{-3}\, d_{rc} \qquad (R^2 = 0.761,\ N = 19) \qquad (5.6)$$

Density per species was estimated counting the number of adults of a given species in the plots. Stand density (D, in $N\,ha^{-1}$), basal area (G, in $m^2 ha^{-1}$), and volume (V, in $m^3 ha^{-1}$) represent the summation of both species.

In order to estimate age and diametric and height increments, cores containing the pith were collected at breast height (1.3m above ground) from all adult trees occurring in both plots (329 adults in total), by a hand–operated, Pressler type increment borer. This sampling height for cores was preferred in order to minimise loss of visible tree rings due to stump rot. Cores were mounted in wooden holders and sanded with successively finer grades of sandpaper, following the procedures of Stokes & Smiley (1968). Annual rings were counted under magnification. Chronological tree age was estimated by adding 15 and 8 years to the age at breast height for *Austrocedrus chilensis* and *Nothofagus dombeyi*, respectively. These periods represented the time needed for individuals of each species to reach core height (1.3m), and they were calculated averaging their height growth rate from 1.3m to h. Particularly, *Austrocedrus chilensis* shows clear growth ring boundaries and therefore is highly suitable for dendrochronological studies

(Villalba 1990, Schweingruber 1993, Villalba & Veblen 1997a,b, Villalba & Veblen 1998, Kitzberger et al. 1995, 1997). A tree may eventually exhibit the phenomenon of both missing and intra–annual rings. Certain dendrochronological techniques, such as cross–dating, can be used to detect them (Stokes & Smiley 1968). In this study, clearly defined growth layers were assumed to be annual for both species. Hence there can be a slight under– or overestimate of ages.

In each plot two subplots of 50x10m were established for estimates of sapling density, one located in the border and the other in the centre of each plot. Saplings were measured for d_{rc} (in cm, recorded to the nearest 0.1 millimetre) with calipers. For estimates of age and growth, outside and near the plots two saplings of each tree species and each d_{rc} class (d_{rc} classes = 1: $0< d_{rc} <0.9$cm, 2: $1<d_{rc}<1.9$,...,10: $9< d_{rc}<9.9$, measured in 40 saplings in total) were sampled by destructive analysis. d_{rc} and h of those saplings were recorded in the field using a measuring tape. The stumps were cut at ground level and growth rings were read in the laboratory. Regression equations relating d_{rc} to the age of adults and saplings were developed to estimate the age of the saplings present in both subplots. For an estimate of the abundance and the spatial distribution of seedling and cotyledonary seedling, inside each plot 50 square subplots of 0.5m^2 each were regularly placed along 5 transects of 50m, by 10m distant from each other. Within these subplots, the species composition of the understorey was recorded. Counting of seedlings and classification of understorey species was carried out first, so as to avoid potential damage during the subsequent fieldwork.

Spatial structure

In each plot, adult stem locations were recorded on a map, determining distances using a measuring tape, and horizontal angles with a compass, in relation to a fixed point with a known relative position. Non–horizontal distances as a result of terrain slope were transformed to horizontal distances by trigonometry. The resulting polar coordinates were converted to rectangular coordinates by trigonometry. The purposes of this mapping were to analyse the tree spatial pattern, e.g., the relative position of trees in the site, and to evaluate a possible association in space between *Austrocedrus chilensis* and *Nothofagus dombeyi* at differently sized squares. The type of the spatial pattern can be random, regular, or clustered. Its intensity is defined by the size of the possible tree patches. Both were assessed using the Morisita's (1959) "index of dispersion" (I_M). This index provides information concerning the way plants are dispersed in space. It is given by:

$$I_M = q\,[\,\Sigma N_y\,(N_y - 1)\,/\,N\,(N-1)\,] \qquad (5.7)$$

in which

I_M = Morisita's index of dispersion,
q = number of squares of the grid covering the plot,
N_y = number of individuals in the square y, and
N = total number of individuals in the whole grid (= ΣN_y).

The index I_M equals 1.0 when the sampled population is randomly dispersed. If plants are clustered, I_M is greater than 1.0; if the population is evenly or hyperdispersed, I_M is less than 1.0.

Because I_M as a function of square sizes provides information on patch sizes (Morisita 1959), the plot map was divided into a grid of squares of increasing size. It was started with squares of 7x7m (51 squares) up to squares of 25x25m (4 squares), with the square size growing by steps of 1m per side (7x7, 8x8,...,25x25m). The relatively low density of both species in the stand made it impossible to estimate indices at square sizes <7x7m, and for each species independently, because the expected square value under randomisation $N / \Sigma q_y$ must be around 3–5 trees per square (Sakai & Oden 1983). Therefore, an indirect approach was used. First, the indices were calculated for the complete data set (including both tree species), with the objective of testing whether all trees together presented a spatial structure. The index was computed for adult trees for each square size and plotted against square size. Total number of individuals considered in the analysis fluctuated because in cases where the total area was indivisible by square size, the index was calculated for the largest subarea containing whole squares of a given size. In this way, fluctuations of I_M related to the shape of the squares (Pielou 1977) were avoided. Significance of departure from randomness of I_M was assessed by a *Chi*–square Test (χ^2) ($P<0.05$), in the following way:

$$\chi^2 = I_M (N - 1) + q - N \tag{5.8}$$

If $\chi^2_{\text{calculated}} > \chi^2_{(q-1,\,0.05)}$, the spatial pattern is not random.

If $\chi^2_{\text{calculated}} \leq \chi^2_{(q-1,\,0.05)}$, the spatial pattern is random.

This analysis was also performed for seedlings and cotyledonary seedlings in order to investigate their spatial distributions. In this case, I_M and its significance was calculated for 100 squares of a size of 0.5m^2, according to eq.(5.7) and (5.8).

Second, a "*Chi*–square test of association" was carried out for different square sizes to investigate the internal structure of the possible clusters, e.g., if they contained mainly one or both species. Each stem map was divided into 100 squares of 25m^2. The frequencies of squares in which both species were present, squares containing only one species, and empty squares were counted. [2x2] contingency tables were created with these presence/absence data. The observed frequencies were compared with the expected frequencies under an independent distribution in space. If *Austrocedrus chilensis* and *Nothofagus dombeyi* tend to occur together either more frequently (positive association) or less frequently (negative association) than expected under a random association, the observed *Chi*–square values will be significantly higher than the expected values. In view of the scale–dependence of the level of association (Kershaw 1973), the analysis was done for different square sizes (5x5, 6x6,...,25x25m). The following equation was used (Kershaw 1973, p.26, Greig–Smith 1983, p.38):

$$\chi^2_{\text{calculated}} = N\,(ad - bc)^2 \,/\, [(a + b)\,(c + d)\,(a + c)\,(b + d)] \tag{5.9}$$

in which

N = total number of subplots,

a = observed number of subplots in which both *A.chilensis* and *N.dombeyi* are present,

b = observed number of subplots whence *A.chilensis* is absent and whence *N.dombeyi* is present,

c = observed number of subplots whence *A.chilensis* is present and whence *N.dombeyi* is absent,

d = observed number of subplots whence both species are absent.

If $\chi^2_{\text{calculated}} \leq \chi^2_{(1, 0.05)}$, there is no spatial association between species.

If $\chi^2_{\text{calculated}} > \chi^2_{(1, 0.05)}$, there is either a positive or a negative association between species.

In cases where there is a positive association in space, $a + d >> c + b$. On the contrary, if there is a negative association $b + c << a + d$. For seedlings and cotyledonary seedlings, a similar test of association was performed in order to examine the spatial relations between species within these development stages. The number of 0.5m^2 subplots in which both species were present and absent was recorded and the data were analysed using eq. (5.9).

Spatial autocorrelation analysis tests whether the observed value of a variable at one locality is independent of values of the variable at neighbouring localities (Sokal & Oden 1978). Using Moran's (1950) "spatial correlation coefficient" $I_A(l)$, the spatial distribution of tree ages for adult *Austrocedrus chilensis* and *Nothofagus dombeyi* trees was evaluated to determine whether or not neighbouring trees were similar to each other with respect to age. This information allows to determine the age structure of eventual tree patches. Neighbouring trees were defined from Euclidean distance classes (l) of three metres ($0<l_1<3$m, $3.1<l_2<6$m,...,$57.1<l_{20}<60$m). For each distance class l, trees a and b were considered neighbours if the distance between them was within the limits of l. For each distance class, the following equation was used:

$$I_A(l) = N\left[\sum\sum w_{ab}\,(x_a - \bar{x})\,(x_b - \bar{x}) \,/\, W \sum (x_a - \bar{x})^2\right] \qquad (5.10)$$

in which:

$I_A(l)$ = Moran's index of spatial autocorrelation for distance class l,
N = total number of mapped tree locations,
x_a = age of the trees at each of the N locations ($a = 1,\ldots,N$),
w_{ab} = 1 if points a and b are neighbours in l, or $w_{ab} = 0$ otherwise,
W = $\sum w_{ab}$, and
$\bar{x}$ = average age of all trees in the plot.

All summations are for a and b, except for cases where $a = b$. For this coefficient, the suitable null hypothesis is the assumption of random distribution, which states that the values of the variable, here tree age, are distributed randomly over the locations. Under this hypothesis Moran's (1950) I_A-coefficient is normal asymptotically distributed with a range of -1 and 1, and with a mean of (Cliff & Ord 1981):

$$E\,[I_A(l)] = -1 \,/\, (N - 1) \approx 0 \qquad (5.11)$$

Values of $I_A(l) > 0$ are termed positively spatially autocorrelated and indicate that trees at a distance l apart tend to be of similar age, whereas values of $I_A(l) < 0$ suggest that trees at a distance l apart tend to be of different ages (negative spatial autocorrelation). The significance of deviation from random expectations in each distance class was tested by calculating the variance of $I_A(l)$ under the assumption of randomisation (in Sokal & Oden (1978), p.210; or in Cliff & Ord (1981), eq.1.39, p.21). Standard normal deviates

$$z(l) = (I_A(l) - E[I_A(l)])(\mathrm{var}\, I_A(l))^{-0.5} \qquad (5.12)$$

were calculated for each l and plotted against l, resulting in a spatial correlogram. The 0.05 significance level of z was used to test significance. Distance classes containing fewer than 20 pairs of neighbouring trees were excluded from analysis because the assumption of normality may be statistically invalid for small groups (Upton & Fingleton 1985, Legendre & Fortin 1989).

Stand and tree growth

Species, time of establishment, and spatial arrangement together account for much of the variation in individual tree growth observed for a particular site (Harper 1977, Silvertown & Lovett Doust 1993). In the present study, individual tree growth is measured as increase in height and stem diameter, whereas stand growth is measured as changes in volume and dry weight of wood. Different approaches were applied in order to examine: a) the overall stand growth, e.g., the growth of the forest and the contribution of each species, b) the genotypic component of growth, e.g., the individual growth rate of the dominant tree species, c) the temporal component of growth, e.g., the growth rate in relation to the age and development stage of individual trees, d) the spatial component of growth, e.g., the individual growth rate of trees in relation to crowding, and e) the individual growth rate in relation to sex classes for the dioecious *Austrocedrus chilensis*.

Overall stand growth (I_v, in $m^3 ha^{-1} yr^{-1}$) (a) represents the summation of adult volume growth for both tree species. For this estimate, the following equation was used (see eq.5.5):

$$i_v = v\, t^{-1} \qquad (5.13)$$

in which:

i_v = mean volume growth of each adult tree ($m^3 yr^{-1}$),
t = age of tree (yr).

Mean individual tree growth in diameter (i_d, in cm yr^{-1}) and height (i_h, in cm yr^{-1}) were used as the basic parameters of individual tree growth (b, c, d). For each adult tree within the plots, and for those saplings analysed by destructive techniques, the variables were estimated by the following equations (see eq.5.1):

$$i_d = d_{rc}\, t^{-1} \qquad (5.14)$$

$$i_h = h\, t^{-1} \qquad (5.15)$$

Mean growth per species (b) represents the average of the increments estimated per tree. To estimate the effects of the time of recruitment of individual plants on growth (c), all trees of a given species were grouped into development stages defined by size (saplings and adults) and age ($1<t_1<40$ yr, $41<t_2<60$, $61<t_3<70$,.., t_8: >110). For each category of size and age, a mean individual growth rate and a measure of variability was calculated per species. In order to compare individual performances in relation to age and development stages of trees, these data were analysed following standard statistical procedures, such as ANOVA and multiple–range tests. To examine the spatial component of tree growth (d), and to detect the main type of the competition process (e.g., symmetric or asymmetric competition), an indirect approach suggested by Cannell et al.(1984) was followed. For instance, a negative relationship between growth performance of a tree and the number of its closer neighbours taller than itself suggests that asymmetric interactions are taking place in the stand (also see van der Hout 1999). This type of relationship is expected when above–ground resources as light are involved in the process. Every adult tree was classified as having either 0, 1, 2, ..., or ≥7 neighbour trees taller than itself, irrespective of the species, within a radius of 5m, which correspond to a surface of 78.5m^2. All the individuals of a given species having the same number of taller neighbours were grouped in a class. Mean radial and height growth rates, and standard errors of the estimates were calculated for all trees in each distance classes (see eq.5.14, 5.15). Then, graphics relating the number of neighbours and growth rates were constructed.

Many studies on dioecious plants claim that females tend to exhibit a slower vegetative growth than males. This is assumed to be caused by their greater allocation of resources to reproduction. In the present study, radial and height growth rates are compared between sexes in *Austrocedrus chilensis*. Individuals holding either male (amentae) or female strobila (cones) were recognised in the field in October and April, respectively. 41 males and 39 females were randomly selected from a sub–population with $d_{rc} \geq 20$cm. For each adult individual sexually identified, the periodic individual diameter growth rate over the last 22 years (i_{d22}, in cm yr^{-1}) was estimated by:

$$i_{d22} = (d_{rc} - d_{rc22})\,t^{-1} \qquad (5.16)$$

in which:

d_{rc} = tree diameter,
d_{rc22} = tree diameter accumulated up to the last 22 years, and
t = number of years ($t = 22$).

The cumulative individual diameter in periods of 5 years (d_{rc}, in cm ind^{-1}) was estimated for 26 males and 22 females, taken from the trees sexually identified (60% of the individuals which sex was previously determined). Growth rates within sex class (i_d, i_{d22}, i_h) were calculated according to:

$$\bar{x} = \Sigma\,(X_i N^{-1}) \qquad (5.17)$$

in which:

$\bar{x}$ = mean value of the growth variable per sex class,
X_i = value of the variable per individual i belonging to a given sex class, and
N = number of individuals in a given sex class.

Minimum area

Based on the concept of "quantitative minimum area" (following Meijer Drees 1954; *ex* Barkman 1989), the statistically optimum plot size for the ecological study of this temperate mixed forest was examined. The continuous variables g_{rc} (eq.5.4), v (eq.5.5), and i_v (eq. 5.13), were asymmetrically distributed to the right (log–normal distribution, *Chi*–square Test, $P<0.05$). Therefore, in order to apply parametric statistics the value of each continuous variable (x_i) was transformed to its logarithm (x_i'), according to the following equation:

$$x_i' = \log_{10}(x_i + 1) \tag{5.18}$$

Then, the transformed variables were normally distributed (*Chi*–square Test, $P<0.05$). In the laboratory, the stem map of plot A was divided to form a matrix containing 100 5x5m–subplots (SP). For each subplot, density (D_{SP}, in ind SP^{-1}), basal area (G_{SP}, in m^2SP^{-1}), volume (V_{SP}, in m^3SP^{-1}), and volume growth (I_{vSP}, in $m^3SP^{-1}yr^{-1}$) were estimated, according to:

$$Y = (\Sigma\, y_i) \tag{5.19}$$

in which:

Y = value of the variable per subplot (e.g., G_{SP}), and
y_i = value of the variable per individual i belonging to a given subplot, regardless of species (e.g., g).

D_{SP} fitted a negative binomial frequency distribution (*Chi*–square Test, $P<0.05$), indicating a clustered spatial pattern at a SP size of 5x5m. Therefore, in order to apply parametric statistical methods, each original value (D_{SP}) was transformed to its logarithm (D'_{SP}), following the recommendation of Krebs (1989, eq.3.18, p.92), according to:

$$D'_{SP} = \log_{10}(D_{SP} + k/2) \tag{5.20}$$

in which k represents the exponent of the negative binomial equation. A maximum likelihood estimate for k was previously estimated by trial and error, following the equation suggested by Krebs (1989, eq.3.13, p.84):

$$S \ln(1 + \bar{N}/k) = \Sigma_{i=0}(A_N / k + N) \tag{5.21}$$

in which:

S = total number of *SP* (*SP*= 100),
N = number of individuals in a given *SP*,
$\bar{N}$ = average number of individuals per *SP*,
A_N = $\Sigma_{j=N+1}(F_j) = F_{N+1} + F_{N+2} + F_{N+3}...,$
i = a counter (0,1,2,3...),
j = a counter (1,2,3,4...), and
F_N = observed number of *SP* containing N individuals.

The data were analysed by the method recommended by Greig–Smith (1952), Kershaw (1973), and Krebs (1989). Changes in the mean values per *SP* of each variable (D_{SP}, G_{SP}, V_{SP}, and I_{vSP}) were examined, randomly selecting the *SP* and combining them progressively to include the total size of the plot. Firstly, 10 *SP* were selected (block size= 10), and the average value per *SP* and the 95% confidence interval were calculated for each transformed variable. In each successive step, the number of *SP* was increased to 20, 30,...,100 (block size= 20, 30,...,100), and a new average and confidence interval were calculated. The confidence interval for the continuous variables (x_i') adjusted to a normal frequency distribution. The confidence interval of D'_{SP} was calculated by the following equation (Krebs 1989, eq.3.20, p.92):

$$D'_{SP} \pm t_\alpha (0.189 \text{ trigamma } (k) / \underline{s})^{0.5} \qquad (5.22)$$

in which:

trigamma (k)= $1/k + 1/2k^2 + 1/6k^3 - 1/30k^5 + 1/42k^7 - 1/30k^9$, and
t_α = t Student value with $\underline{s}$-1 degrees of freedom for α= 0.05
$\underline{s}$ = number of *SP* involved in each estimate.

Means and confidence intervals of all variables were re–transformed to the original scale by the inverse function (log–antilog). Graphs relating the value of the variables in relation to block size were constructed. The accuracy level of the estimates of D_{SP}, G_{SP}, V_{SP}, and I_{vSP} was measured as the relative error (RE), by:

$$\text{RE } (\%) = 100\ (t\, s_{\bar{x}} / \bar{x}) \qquad (5.23)$$

Stand patterns and processes: results and discussion

Site characteristics

The fieldwork was carried out in the Nahuel Huapi National Park, a natural reserve of 7,641km^2 located in northwestern Patagonia. In the reserve, *Austrocedrus chilensis* and *Nothofagus dombeyi*–dominated forests cover 148.4km^2 (1.9% of the reserve area) and 1,079.5km^2 (14.2%), respectively. The rest of the area is covered by 21.0% of *Nothofagus pumilio* forests, 20.3% of shrublands, 16.8% of alpine vegetation, 10.1% of water bodies, 7.5% of steppes, 4.7% of urban areas, and 3.5% of peatlands (Mermoz & Martín 1987). The sampling site is located at 41°11'S and 71°25'W, at an altitude of 950m on a northern slope of Mt.Catedral (2,388m), near the western side of lake Gutiérrez (figure 10). Mean annual temperature and precipitation are 8°C and 1,600mm, respectively (De Fina 1972, Barros et al. 1983, Cordon et al. 1993). Within the plots, slopes varied between 11° and 17° following a south–north direction. The soil is an Andosol (FAO–UNESCO Soil Classification System, FAO 1990) (INTA 1991). The mixed stand selected for sampling is situated within a steep environmental gradient, largely determined by a variation in rainfall and its seasonal distribution bulk, estimated to change at a rate of 70mm km^{-1} (figure 7). This striking spatial gradient is reflected in a continuum variation in plant abundance, composition, and richness, and therefore in the structure and physiognomy of vegetation, as found in West Africa by van Rompaey (1993). The more xeric *Austrocedrus chilensis* and the more mesic *Nothofagus dombeyi* form a transitional association between two different community types, the Valdivian rain forests toward the west and the Patagonian steppe toward the east (figures 6, 7). Both tree species tend to spread with population maxima situated at different positions within this ecological transition zone, with no distribution being exactly equal, as *Austrocedrus chilensis* dominates the stands toward the east and *Nothofagus dombeyi*

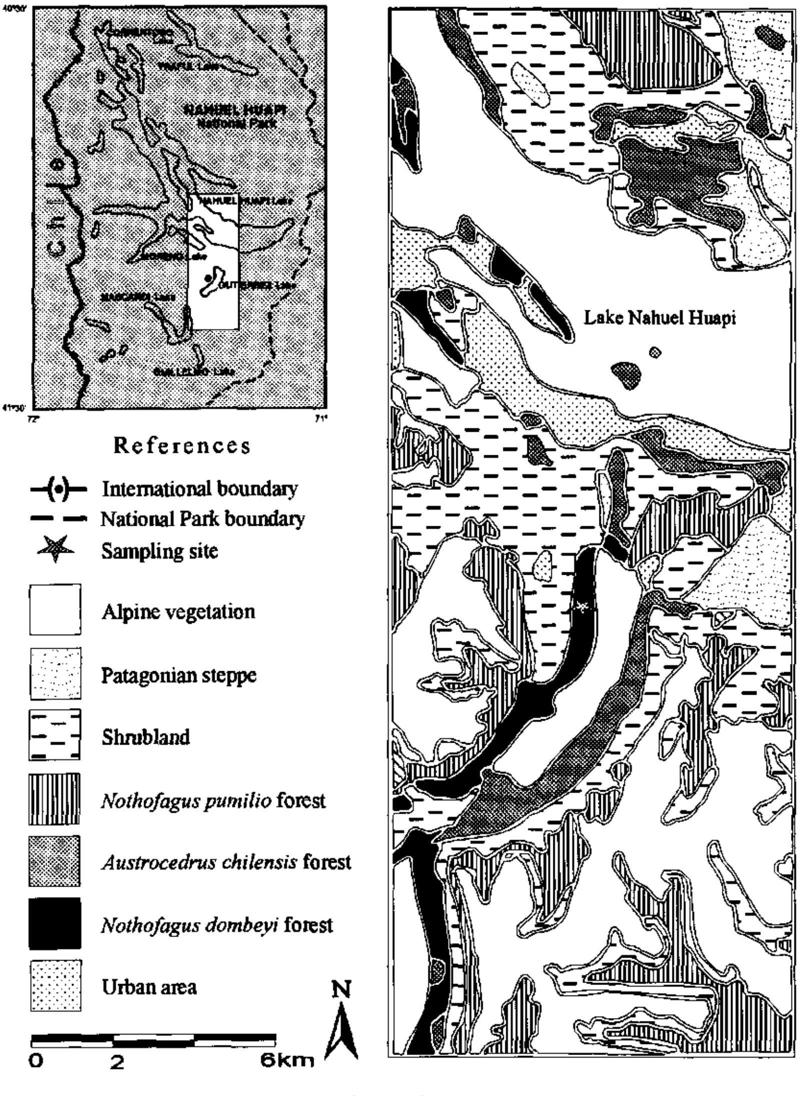


Figure 10: Location of the sampling site and the current vegetation types in the study area (APN 1986). For general position see maps of southern South America (figure 1) and western Patagonia (figure 6).

toward the west. However, their niches overlap in a narrow fringe in–between the annual isohyets of 1,400 and 1,800mm (figures 6, 7). Displacement of the ecotone position occurred at least within the last 100 years, a phenomenon reflected in a re–expansion of arborescent flora toward the east, mainly caused by the alleviation of human impact (Veblen & Lorenz 1988).

Within the plots 51 vascular plants are found, from which 46% are hemicryptophytes, 32% phanerophytes, 8% lianas, 8% geophytes, 2% chamaephytes, 2% epiphytes, and 2% geophytes (table 20, figure 11). This biological spectrum represents the proportion of each of the

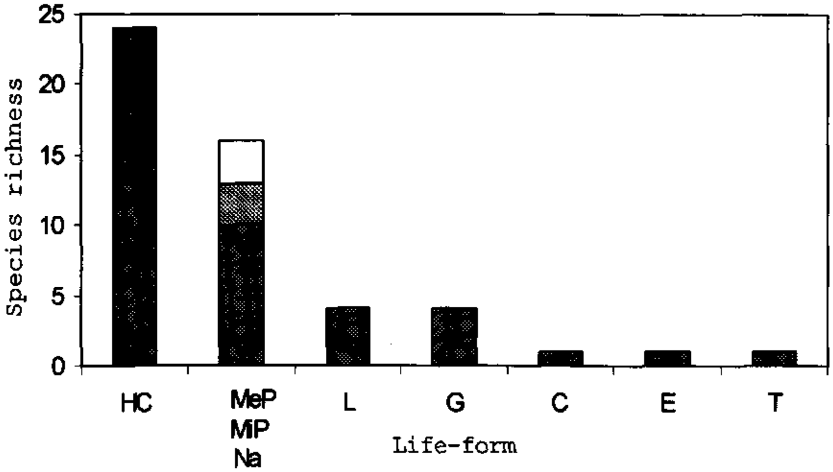


Figure 11: Spectrum of biological types in the vascular flora within the study site. It represents the proportional contribution of each of the Raunkiaer's (1934) life forms to the community.

Raunkiaer's physiognomic life-form classification of vascular terrestrial plants comprises: self-supporting plants, woody or herbaceous perennials <0.5m height (Chamaephytes, C), 0.5–2m high (Nanophanerophytes, NaP), 2–5m high (Microphanerophytes, MiP), 5–50m high (Mesophanerophytes, MeP), and >50m high (Megaphanerophytes, MgP) (NP). Herb plants include annuals (Therophytes, T) or perennials with shoot reduction having bodies either above the ground (Hemicryptophytes, HC), or bellow the ground (Geophytes, G). Plants without self-support include those which either germinate on the soil and roots keep a permanent contact with it (Lianas, L), or germinate and develop upon the host plant and a contact with the soil is never established (Epiphytes, E). Hemiepiphytes (He) comprises plants that either germinate on a host and become connected with the soil later, or germinate on the soil, climb upon a host and thereafter lose contact with the soil. This last category is not present within the study site.

Raunkiaer's (1934) life forms within the community. It is clearly dominated by hemicryptophytes and phanerophytes. This agrees with those found in other zonal sites within the subantarctic forests. For instance, in the Manso Superior river basin (71°53'–71°36'W and 41°19'–41°08'S, Nahuel Huapi National Park), from the 327 vascular species identified 55.3% are hemicryptophytes and 17.1% phanerophytes (Gómez & Gallopín 1982). Within the study site, the only two mesophanerophytes are those dominating the stand (table 20). The forest understorey is made up of potential trees (*sensu* Oldeman 1990) of *Austrocedrus chilensis* and *Nothofagus dombeyi*, together with some scattered low trees of the species *Aristotelia chilensis* (Elaeocarpaceae), *Embothrium coccineum* and *Lomatia hirsuta* (Proteaceae), and *Schinus patagonicus* (Anacardiaceae), as shown in table 20. The most abundant families within the study site are Compositae (10 species), Gramineae (5), and Rosaceae (3). Only 4 non–indigenous species are found in the site (8% of the total plant richness). However, they comprise a limited abundance and biomass (table 20). The more abundant shrubs are *Maytenus chubutensis*, *Berberis buxifolia*, *Berberis darwinii*, and *Ribes magellanicus*. The bamboo *Chusquea culeou* is concentrated in small patches in the lower parts of the site. Dominant herbs are *Poa spp.* (Gramineae), *Acaena pinnatifida* (Rosaceae), *Baccharis spp.*, *Mutisia spp.*, *Adenocaulon chilense* (Compositae), *Alstroemeria aurantiaca* (Amaryllidaceae), *Eryngium paniculatum*,

Table 20: Composition of vascular plants in the study plot. Life forms (LF, Raunkiaer 1934) and species origin (N: native, EA: Eurasia, E: Europe, NA: North Africa) (Brión et al.1987) is indicated. For references on LF see figure 11.

Family	Species	LF	Origin
Rosaceae	*Acaena pinnatifida*	HC	N
Compositae	*Adenocaulon chilense*	HC	N
Graminae	*Agrostis spp*	HC	N
Amaryllidaceae	*Alstroemeria aurantiaca*	G	N
Ranunculaceae	*Anemone multifida*	HC	N
Elaeocarpaceae	*Aristotelia chilensis*	MiP	N
Cupressaceae	*Austrocedrus chilensis*	MeP	N
Compositae	*Baccharis magellanica*	C	N
Compositae	*Baccharis romboidalis*	NaP	N
Geraniaceae	*Balbicia gracilis*	HC	N
Berberidaceae	*Berberis buxifolia*	NaP	*N*
Berberidaceae	*Berberis darwinii*	NaP	N
Blechnaceae	*Blechnum auriculatum*	HC	N
Scrophulariaceae	*Calceolaria corimbosa*	HC	N
Caryophyllaceae	*Cerastium arvense*	HC	EA
Orquidaceae	*Chloraea chica*	G	N
Graminae	*Chusquea culeou*	NaP	N
Polemoniaceae	*Collomia biflora*	T	N
Compositae	*Conyza chilensis*	HC	N
Cyperaceae	*Eleocharis pachycarpa*	HC	N
Graminae	*Elymus caudatum*	HC	N
Proteaceae	*Embothtrium coccineum*	MiP	N
Umbelliferae	*Eryngium paniculatum*	HC	N
Rosaceae	*Fragaria chiloensis*	HC	N
Orquidaceae	*Gavilea lutea*	G	N
Geraniaceae	*Geranium patagonica*	HC	N
Compositae	*Hieracium prealtum*	HC	N
Compositae	*Hypochoeris radicata*	HC	EA/NA
Juncaceae	*Juncus stipulatus*	HC	N
Compositae	*Leuceria achillaeifolia*	HC	N
Proteaceae	*Lomatia hirsuta*	MiP	N
Celastraceae	*Maytenus boaria*	MeP	N
Celastraceae	*Maytenus chubutensis*	NaP	N
Misodendraceae	*Misodendrum punctulatum*	E	N
Compositae	*Mutisia spinosa*	L	N
Compositae	*Mutisia decurrens*	L	N
Santalaceae	*Myoschilos oblongum*	NaP	N
Nothofagaceae	*Nothofagus dombeyi*	MeP	N
Umbelliferae	*Osmorrhiza chilensis*	HC	N
Ericaceae	*Pernettya mucronata*	NaP	N
Graminae	*Poa spp.*	HC	N
Aspidiaceae	*Polystichum plicatum*	HC	N
Rubiaceae	*Relbunium hypocarpium*	L	N
Saxifragaceae	*Ribes magellanicum*	NaP	N
Rosaceae	*Rosa rubiginosa*	NaP	E
Polygonaceae	*Rumex acetosella*	HC	EA
Anacardiaceae	*Schinus patagonicus*	NaP	N
Compositae	*Solidago chilensis*	G	N
Graminae	*Trisetum caudatum*	HC	N
Leguminosae	*Vicia nigricans*	L	N
Violaceae	*Viola maculata*	HC	N

Osmorhiza chilensis (Umbelliferae), *Vicia nigricans* (Leguminosae), and the fern *Blechnum auriculatum* (Blechnaceae). Moss cover is present in some areas. No evidence of small–scale tree–falls is observed in the plots. Two *Austrocedrus chilensis* (d_{rc}= 35.0 and 32.8cm) had died but were still standing.

Stand structure

Performance structure

A summary of the stand structure is shown in table 21. In plot A, total density is estimated to be 12,548 ind ha^{-1}, from which 6.2, 25.5, and 68.3% correspond to adult, sapling, and seedlings, respectively. In abundance, the plot is dominated by *Austrocedrus chilensis*, which contributes with 78.4% to the total density of adults estimated to be 776 ind ha^{-1}. For *Austrocedrus chilensis* and *Nothofagus dombeyi*, density of saplings is 361 (11.3% of total sapling density) and 2,840 ind ha^{-1} (88.7%), respectively. These figures indicate that within this plot, the understorey is occupied almost exclusively by *Nothofagus dombeyi* saplings, whereas the overstorey is dominated by *Austrocedrus chilensis*. For *Austrocedrus chilensis*, the ratio between adults and saplings is 1.68 whereas for *Nothofagus dombeyi* is 0.06, indicating that the population of the former species is mainly composed of adults and that of the latter species of saplings. Total basal area is 67.8m^{2}ha^{-1}, of which *Austrocedrus chilensis* contributes with 67.7%. Total volume is estimated to be 542.6m^{3}ha^{-1}, of which the conifer represents 68.0%. In plot B, total density is estimated to be 9,034 ind ha^{-1}, of which around 6% corresponds to adult trees, 30.8% to saplings, and 63.2% to seedlings. Between species, the adult class is highly balanced in abundance: *Austrocedrus chilensis* contributes with 268 ind ha^{-1} (49.6% of total density) and *Nothofagus dombeyi* with 272 ind ha^{-1} (54.4%). The ratio between adults and saplings is 0.21 and 0.18 for *Austrocedrus chilensis* and *Nothofagus dombeyi*, respectively, which indicates in both species an equivalent distribution within size classes. Total basal area and volume are estimated in 66.8m^{2}ha^{-1} and 674.8m^{3}ha^{-1}, respectively. *Nothofagus dombeyi* contributes to plot B with the largest biomass, attaining 62.2% of the total volume.

In plot A, adult d_{rc} is rather similar in *Austrocedrus chilensis* and *Nothofagus dombeyi* (table 21). However, the latter species shows a higher variability in size and accounts for the biggest individual tree with a d_{rc}= 100.0cm. The biggest *Austrocedrus chilensis* exhibits a d_{rc}= 57.5cm. The diameter–class frequency distribution shows that *Nothofagus dombeyi* dominates the biggest d_{rc} classes (d_{rc}> 60cm) (figure 12A). The comparatively high proportion of trees belonging to the smallest size class ($10<d_{rc}\leq 19.9$cm) is caused by trees of the understorey cohort that entered into the adult population. *Austrocedrus chilensis* dominates the size classes d_{rc}< 60cm. *Austrocedrus chilensis* population has an asymmetric, positively skewed distribution of plant sizes, with a relatively small number of large plants and many small ones. A size hierarchy, such as that clearly observed in the even–aged population of *Austrocedrus chilensis* (see subsequent paragraphs, table 21, figure 13A), arises when bigger trees also grow at faster rates as a result of their larger exposition to full sunlight (Hutchings 1997). In plot B, *Austrocedrus chilensis* exhibits the largest mean diameter (d_{rc}= 40.7cm) and the biggest trees of the plot (d_{rc}= 116.9cm). Its size frequency follows a normal, symmetric, bell–shaped distribution (Kolmogorov– Smirnov Test, $P<0.05$) (figure 12B). In *Nothofagus dombeyi*, plant sizes in plot B follows a *L*–shaped

Table 21: Summary of the stand structure and growth for plots A and B. Total values and percentages (in brackets) at stand level (density (N), basal area (G), volume (V), dry-weight timber biomass (B)[(a)], and stemwood growth in volume and dry-weight (I_V)), and mean values at individual level (root collar diameter (d_{rc}), total height (h), and age) are indicated for species and development stages (SL: seedling, SE: sapling, AD: adult). Mean ($\bar{X}$), standard error (SE) and range (R) of the variables is also indicated.

Variable	Stage		Plot A			Plot B		
			A.chilensis (%)	*N.dombeyi* (%)	Total	*A.chilensis* (%)	*N.dombeyi* (%)	Total
N (ind/ha)	SL		2,857 (33.3)	5,714 (66.7)	8,571 (100)	2,040 (35.7)	3,674 (64.3)	5,715 (100)
	SP		361 (11.3)	2,840 (88.7)	3,201 (100)	1,260 (45.3)	1,520 (54.7)	2,780 (100)
	AD		608 (78.4)	168 (21.6)	776 (100)	268 (49.6)	272 (50.4)	540 (100)
	T		3,826	8,722	12,548	3,568	5,466	9,034
G (m^2/ha)	AD		48.9 (67.7)	18.9 (32.3)	67.8 (100)	39.4 (59.0)	27.4 (41.0)	66.8 (100)
V (m^3/ha)	AD		369.1 (68.0)	173.5 (32.0)	542.6 (100)	254.8(37.8)	420.0 (62.2)	674.8 (100)
B (T/ha)	AD		143.9 (58.4)	102.4 (41.6)	246.3 (100)	99.4 (28.6)	247.8 (71.4)	347.2 (100)
Iv (m^3/ha/yr)	AD		3.6 (57.0)	2.8 (43.0)	6.4 (100)	2.5 (30.4)	5.6 (69.6)	8.1 (100)
Iv (T/ha/yr)	AD		1.40 (45.2)	1.65 (54.8)	3.05 (100)	0.98 (22.9)	3.30 (77.1)	4.28 (100)
d_{rc} (cm)	AD	$\bar{X}$	30.8	32.6		40.7	28.6	
		SE	0.9	4.2		1.8	2.6	
		R	10.0-57.5	10.0-100.0		13.1-116.9	10.0-108.3	
		N	152	42		67	68	
H (m)	AD	$\bar{X}$	15.9	14.9		15.6	13.4	
		SE	0.4	1.4		0.3	0.6	
		R	6.4-27.0	5.8-38.0		5.4-21.6	4.9-26.3	
		N	152	42		67	68	
Age (yr)	AD	$\bar{X}$	99.1	49.5		100.7	50.4	
		SE	0.8	5.0		1.6	2.8	
		R	62-127	19-136		63-176	29-152	
		N	152	42		67	68	

(a) Specific dry weight of wood for *Austrocedrus chilensis* is 0.39g cm^{-3}, for *Nothofagus dombeyi* is 0.59g cm^{-3} (Anonymous 1994).

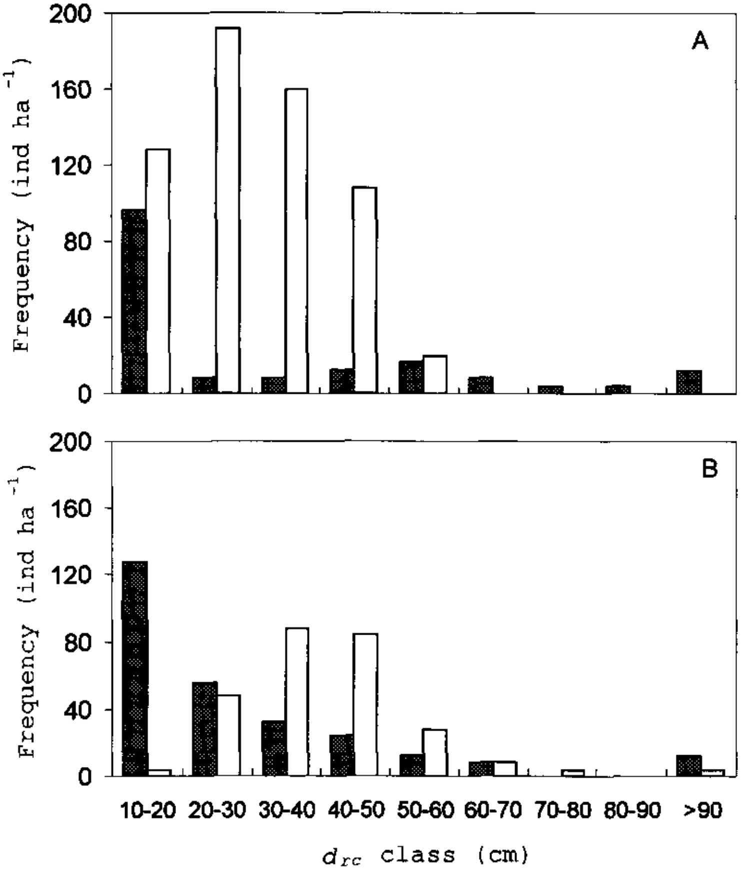


Figure 12: Root collar diameter (d_{rc})-class frequency distribution for adults of *Austrocedrus chilensis* (empty bars; plot A N= 152, plot B N= 67) and *Nothofagus dombeyi* (shaded bars; plot A N= 42, plot B N= 68), in the 50x50m sample plots A and B.

distribution with abundance of smaller trees and scarcity of bigger trees.

In plot A, mean height is similar in both populations with *H*= 15.9m for *Austrocedrus chilensis* and *H*= 14.9m for *Nothofagus dombeyi*. However, the latter species shows the highest individual with *h*= 38m, which is 11m higher than the highest *Austrocedrus chilensis* (table 21). There is a quite clear segregation of species amongst vertical layers, resulting in a multi–canopied stand (figures 14A, 15A). The understorey in between 0.5m and 5m height is almost exclusively dominated by juveniles of *Nothofagus dombeyi* comprising 89% of the trees within this height range. The intermediate stratum of 5-10m height is dominated by both tree species in the same proportion. The upper continuous stratum between 10-25m height is predominantly made up of *Austrocedrus chilensis*, accounting for 87% of the total number of trees within this range. On the contrary, the emergent, discontinuous stratum between 25-40m height is almost entirely

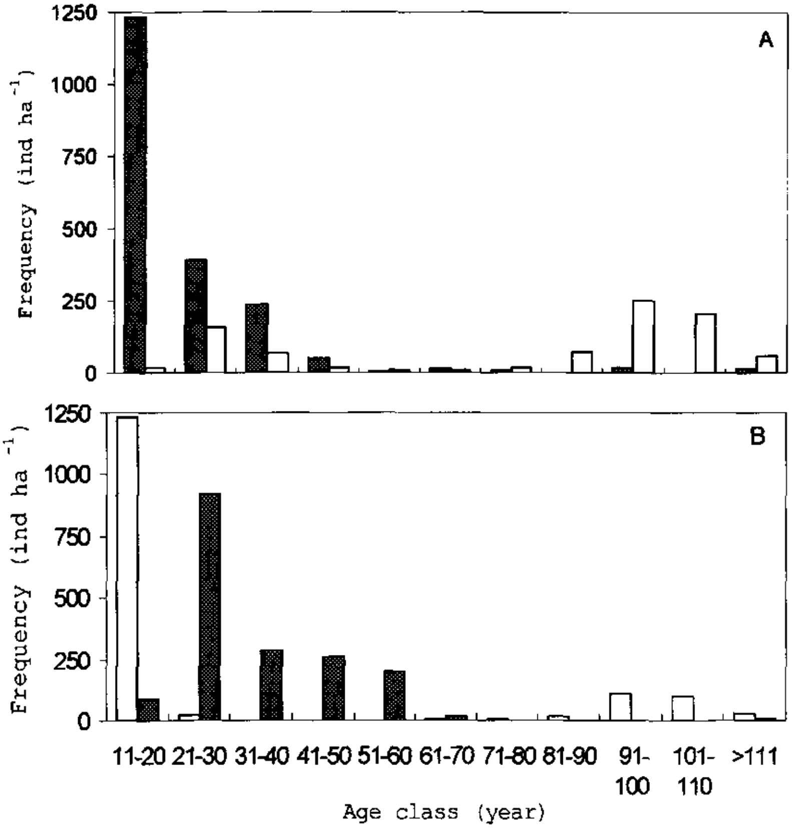


Figure 13: Chronological age-class frequency distribution of *Austrocedrus chilensis* (empty bars) and *Nothofagus dombeyi* (shaded bars), in the 50x50m sample plots A and B.

occupied by scattered *Nothofagus dombeyi* trees with very expanded crowns (78% of the total number of trees within this height range). The population of *Austrocedrus chilensis* is concentrated in the 10–25m–height range, in which 90% of its adult individuals are found. The population of *Nothofagus dombeyi* is concentrated in the 5–20m–height range (79% of its individuals), with a peak of 36% in the 5–10m height class. In comparison with plot A, plot B shows a lower height (table 21), a weaker vertical development (figures 14B, 15B), and a more balanced stratification. A mean height of 15.6m and 13.4m is estimated for *Austrocedrus chilensis* and *Nothofagus dombeyi*, respectively, and the height range in between 30 and 40m is absent. *Nothofagus dombeyi* dominates the tallest and lowest height classes within this plot, whereas the height class 10–25m is occupied by both species in the same proportion.

The current stratification of the canopy, in which each species tends to occupy space in a different layer, has largely occurred in plot A whereas in plot B the process is still ongoing (figures 14, 15). This process is primarily caused by the combination of three interrelated

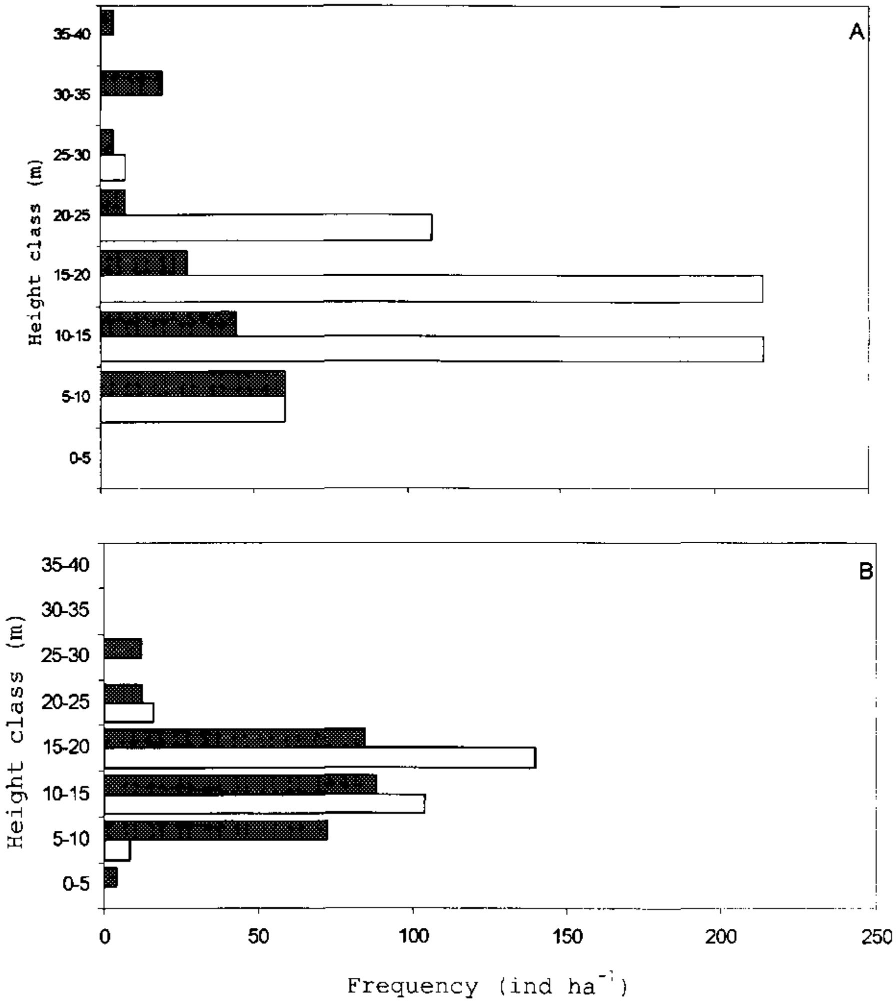


Figure 14: Total height (h)-class frequency distribution for adults of *Austrocedrus chilensis* (empty bars; plot A N= 152, plot B N= 67) and *Nothofagus dombeyi* (shaded bars; plot A N= 42, plot B N= 68), in the 50x50m sample plots A and B.

processes. The first one is the inherent differences in height growth between species. For instance, adults of *Nothofagus dombeyi* exhibit a mean height growth of 29.3cm yr^{-1}, whereas of *Austrocedrus chilensis* 15.8cm yr^{-1}, see Growth and interaction). The second process is the differential recruitment of saplings of both species along time, resulting in a double–cohort stand (see Age structure). Finally, the ability of low individuals to tolerate their suppressed social position. As forest development proceeds, its vertical building will display marked changes as a results of non–random, density–dependent mortality by self–thinning, density–independent mortality following tree maturation and senescence, and patch formation. Within species,

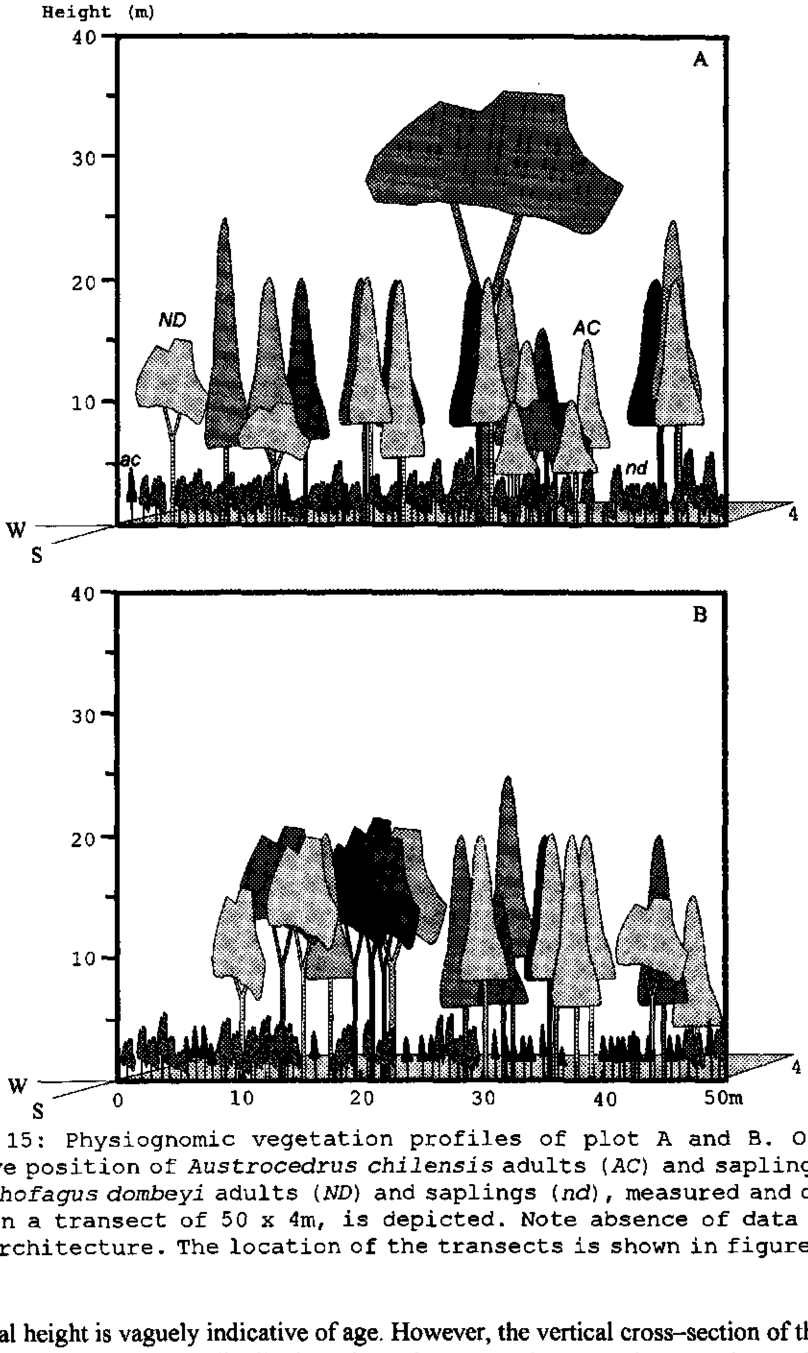


Figure 15: Physiognomic vegetation profiles of plot A and B. Only the relative position of *Austrocedrus chilensis* adults (*AC*) and saplings (*ac*), and *Nothofagus dombeyi* adults (*ND*) and saplings (*nd*), measured and drawn to scale in a transect of 50 x 4m, is depicted. Note absence of data on tree crown architecture. The location of the transects is shown in figure 17.

differential height is vaguely indicative of age. However, the vertical cross–section of the plots is not a criterion of stand age distribution given the contrasting growth rates observed between species (see Growth and interaction). For instance, plot A is distinctly irregular in height, a pattern expected to occur in uneven–aged stands. However, the *Nothofagus dombeyi* trees in the upper stratum have the same age as all the *Austrocedrus chilensis* trees in the lower stratum (figure 15A). Plot B has an all– but smooth upper canopy of narrow–crowned trees with a continuous stratum at 20m, as expected in even–aged stands. However, adult trees of *Nothofagus dombeyi* exhibit a mean age that is half than those of *Austrocedrus chilensis* trees (figure 15B) (see Age structure).

Age structure

For *Austrocedrus chilensis*, mean age of adults is 99 and 101 years for plot A and B, respectively. For *Nothofagus dombeyi*, mean age is 50 years for both plots A and B (table 21). Age of saplings was assessed by the following regressions (figure 16):

for *Austrocedrus chilensis*: $d_{rc} = 7.5 * 10^{-4}\, t^{2.297}$ ($R^2 = 0.807$, N= 172) (5.24)

for *Nothofagus dombeyi*: $d_{rc} = -10.2 + 0.830\, t$ ($R^2 = 0.920$, N= 62) (5.25)

A cohort is an aggregation of trees that starts as a result of a single impact ("zero event", *sensu* Oldeman 1990). In plot A, the bimodal age–class frequency distribution of *Austrocedrus chilensis* is a consequence of the presence of two distinct and non–overlapping cohorts: a post–fire and an understorey cohort (figure 13A; see Stand dynamics). The post–fire cohort is exclusively constituted by adults ($d_{rc} \geq$ 10cm) with an age range of $60 > t > 110$ years, which had arisen since around 1860. Nevertheless, most of the trees became established in a relatively short period between 1885 and 1905, when nearly 80% of the present adult trees colonised the site. During the following years, the establishment of new individuals was rather low, and the last living adults arrived around 1930. The understorey cohort, made up entirely of saplings ($d_{rc} <$ 10cm, $h \geq$ 50cm), arose around fifty years ago. Maximal recruitment occurred between 1965 and 1975, when nearly 60% of the present saplings entered the stand. In this species, the age structure of both cohorts follows a normal distribution (Kolmogorov–Smirnov Test, $P<0.05$). For *Nothofagus dombeyi*, two cohorts can be identified as well. However, they exhibit a different structure compared with that of *Austrocedrus chilensis* (figure 13A). A very small cohort with a normal age structure (Kolmogorov–Smirnov Test, $P<0.05$) became established after a fire. The last trees were recruited around 1930. However, new recruitment began to increase rapidly since ca.1940 when the understorey cohort began to join the earlier population; for instance, more than 80% of *Nothofagus dombeyi* population became established in the last thirty years. Because of their recently increasing rate of colonisation, the understorey cohort shows a "*L*–shaped", highly positively skewed age–class frequency distribution. For analogous development in northern mixed *Fagus* stands, see Peters (1997).

In plot B, a double–cohort population is observed for *Austrocedrus chilensis* (figure 13B). The post–fire cohort exhibits an age range of 70 to >110 years, arranged following a normal statistical distribution (Kolmogorov–Smirnov Test, $P<0.05$). Maximal recruitment occurred also from 1885 to 1905, when around 80% of the member of this cohort became established. Within this range, all the trees are interpreted as belonging to the same generation except for the oldest *Austrocedrus chilensis* recorded within the plot and the stand. It exhibits an age of 176 years that differs from the second oldest *Austrocedrus chilensis* tree found in the stand by some 60 years. This earliest member of the *Austrocedrus chilensis* population can be interpreted as a veteran

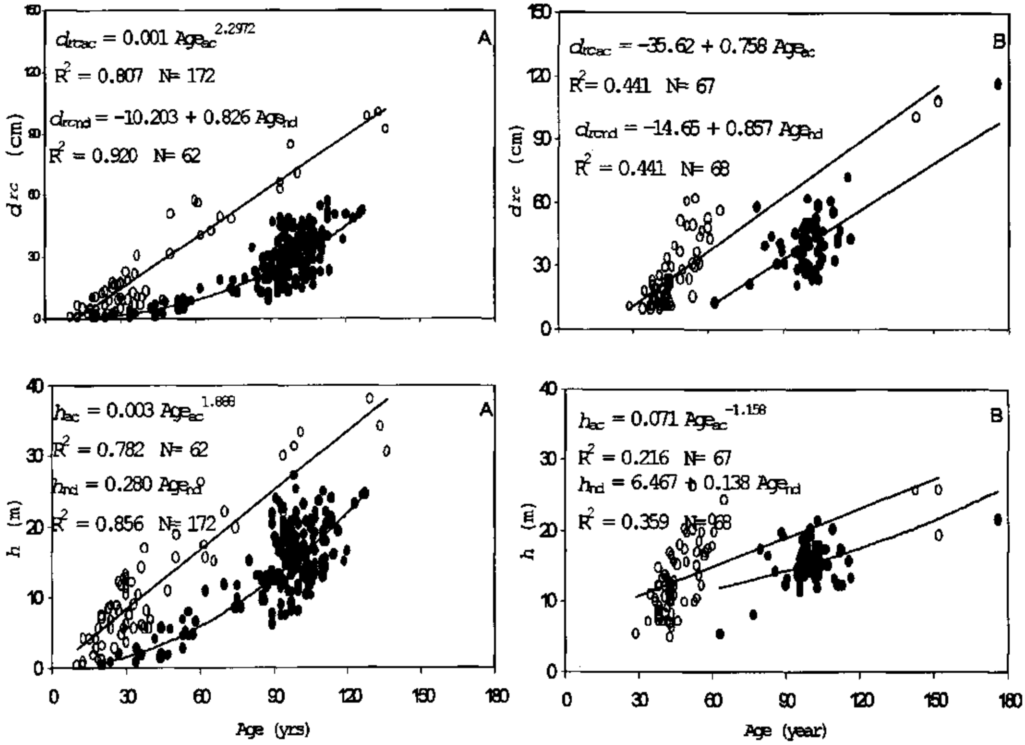


Figure 16: Allometric relationships between root collar diameter (d_{rc}) and total height (*h*), in relation to age for individuals of *Austrocedrus chilensis* (*Ac*, shaded circles) and *Nothofagus dombeyi* (*Nd*, empty circles), located in plots A and B. The equation of simple regression ($P<0.05$), the regression coefficient (R^2), and the sample size (N) is also indicated.

tree of a pre–disturbance cohort that must have survived the original fires. There are no *Austrocedrus chilensis* trees belonging to ages ranging from 30 to 60 years. The understorey cohort is well represented by trees within the age class from 11 to 20 years, with 1,232 ind ha^{-1} (80% of the total density of this species). These trees represent a second regeneration pulse occurring since 1980. *Nothofagus dombeyi* is scarcely represented within the overstorey cohort as only 3 individuals, all of them with ages from 143 to 152 years, are found (figure 13B). They probably represent survivors of the destruction that initiated the present stand, as inferred by the fire scars observed on the stems. Successful colonisation and persistence of *Nothofagus dombeyi* began around 1930, composing a large understorey cohort with ages varying between 11 and 70 years.

From a combined analysis of plot A and B, a common pattern of age structure arises. Two main regenerative events have occurred in the stand: a first event, around 130 years ago, gave origin to a post–fire cohorts in both species, and a second event, started some 50 years ago beneath the previous one, is represented by a re–initiation cohort. As a consequence of both pulses, at present a double–cohort stand is perceived. There is a contrasting pattern of regeneration between species, as reflected by their relative abundance in each cohort. During the initial stages of forest development, *Nothofagus dombeyi* experienced establishment failures while *Austrocedrus chilensis* displayed a more intense process of colonisation and persistence. During the first 60 years of stand development, the species composition remained almost entirely dominated by the initial, post–fire population of *Austrocedrus chilensis*. Such a condition would indicate that this physical factor had favoured the conifer or restricted the broadleaved species. However, during the last 60 years a process of rapid colonisation occurred, particularly by *Nothofagus dombeyi*, as proven by the current age distributions.

Spatial structure

A tree base map of adult *Austrocedrus chilensis* and *Nothofagus dombeyi* trees is given in figure 17. In plot A, two distinct spatial configurations can be seen on the map: individuals are grouped, and the groups are mainly placed in the lower, southern part of the plot (figure 17A). For adult trees of both species, the values of Morisita's (1959) *IM* index significantly differ from 1 up to a square size of 16x16m, which demonstrates that individuals are contagiously dispersed with a mean patch size of 256m^2 (figure 18). The indices are significant at larger square sizes (e.g., >20x20m) because the clusters are not evenly distributed in space, and therefore the indices do not indicate the patch size, but a mean square surrounding at least one patch. Examining the stem map, patch sizes are variable with rather isolated, small clusters as well as larger patches. In plot B, a contagious spatial pattern can also be seen by eye in the stem map (figure 17B). For all trees together, *IM* again indicates a mean size of around 16x16m for clusters (figure 18). The spatial pattern of seedlings is also characterised by patchiness, in this case at a square size of 0.5m^2. For instance, for *Austrocedrus chilensis* *IM* = 3.03 and χ^2= 131.3 (χ^2(99, 0.05)= 123.2), and for *Nothofagus dombeyi* *IM*= 10.3 and χ^2= 350.1 (χ^2(99, 0.05)= 123.2). The outcomes of the combined analysis of spatial pattern and association are: i) when the adults of both species are considered together, the dispersion indices show trees to grow in patches at an intensity of around 250m^2 (figure 18). For seedlings distribution, patchiness was also found in both tree species. For adults and seedlings, there is no spatial association, neither negative nor positive, between species within the patches analysed at different square sizes (*Chi*–square Test, $P<0.05$) (tables 22, 23). In summary, the results indicate that in the study plots trees are aggregated in patches and these patches have a random composition of species.

The spatial structure of a population is related to morphological (e.g., tree architecture, vegetative reproduction, seed weight), environmental (reflecting the compound nature of the environmental factors), and interaction–related factors (e.g., self–thinning in denser patches, pollination, shade pattern and seedlings) (Kershaw 1973, Oldeman 1990, Vester 1997). The dynamics of spatial arrangement is a consequence of the modification of the pattern of recruitment by mortality factors (Hutchings 1997) and the architectural dynamics of trees (Oldeman 1990, Peters 1997). Williamson (1975) found that adult trees of early successional species exhibited maximal clumping at square sizes corresponding to the sizes of light–gaps created by treefall, but the dominant species showed a random pattern. Whipple (1980) and Good & Whipple (1982) found that the dispersal patterns in individuals of dominant populations tended to decrease in degree of clumping with increasing tree size, because of differential mortality incurred as the stems increase in size. In an old–growth Valdivian forests, Veblen et al.(1980) found a clumped pattern among shade–tolerant late successional species, growing in

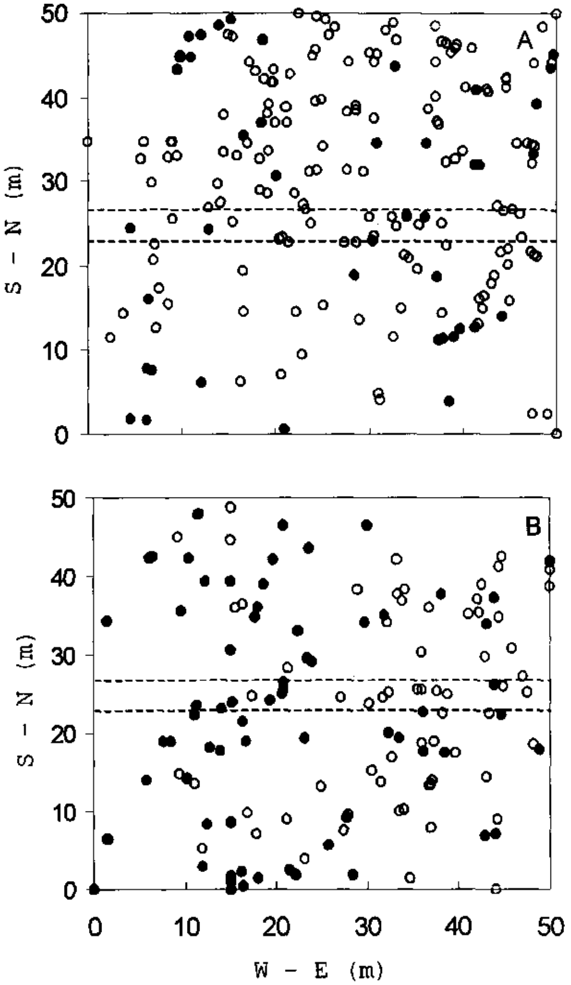


Figure 17: Maps of the 50x50m sample plots A and B, showing the location of adults of *Austrocedrus chilensis* (empty circles; plot A N= 152, plot B= 67) and *Nothofagus dombeyi* (shaded circles; plot A N= 42, plot B N= 68). Topographic directions are shown on the axis. Dashed lines indicate the part of the plots depicted in the profiles of figure 15.

gaps created by the uprooting of *Nothofagus* trees. Armesto et al.(1986) found that the spatial structures of forests is independent from the latitudinal location of stands, that the pattern for a particular species vary between environmentally different sites, and that the structure is not correlated with a particular seed dispersal mechanism. Our figure 15B shows how relatively large early clusters can break up in smaller–sized patches by uneven–aged mortality of the big trees from early clusters. Vester (1997) explained the mechanism of selective mortality in more complex Colombian secondary rainforests on abandoned agricultural fields.

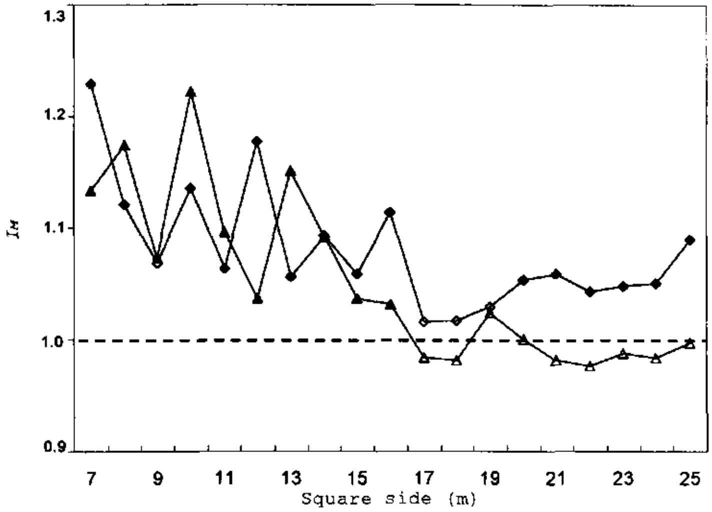


Figure 18: Values of Morisita's index of dispersion (*IM*; Morisita 1959) calculated at different square sizes for adults of *Austrocedrus chilensis* and *Nothofagus dombeyi* located in plot A (rhomboids) and B (triangles). Square axis indicates the length of the side of a square, in meters. Filled marks indicate an *IM* significantly greater than 1.0 (horizontal dotted line), otherwise *IM* does not differ significantly from 1 (χ^2-Test, $P<0.05$).

Indeed, since the recognition that after large–scale impacts similar structures and processes occur in divergent forest types, a conceptual model of forest development involving four distinct but fuzzy phases has been postulated by different authors (Hallé et al. 1978, Bormann & Likens 1979, Oliver 1981, Peet & Christensen 1987, and with a different scale concept Oldeman 1983, 1990). This model also predicts changes in distributional patterns of trees related to the development phase of the forest (Peet & Christensen 1987, Oldeman 1990). Because seed dispersal is not spatially homogeneous and distribution of microsites for establishment is often quite patchy, trees are expected to have a clumped arrangement up to the initiation of the second phase of forest development, which is characterised by the closure of the canopy and by a density–dependent self–thinning process, with an increase of biomass of the surviving trees. During the second phase, it is predicted that tree pattern shifts from clumped to regular to random as a consequence of both mortality and crown development, related to re–allocation of space and resources. With continued forest development, seedlings and saplings typically occur again in patches where canopy trees die, so spatial patterns shift back towards greater clumping. For instance, patches of various sizes and ages are characteristic of the old growth steady–state forest (or "eco–units" in a "silvatic mosaic" *sensu* Oldeman 1990) dominated by gap replacement processes. This stage is reached as long as major impacts do not hit the area. The data suggest that a microspatial heterogeneity of the environment is the cause of the observed clumped spacing of the trees. This is because both tree species exhibit only a sexual mechanism of reproduction, and because trees became established after the complete elimination of the original vegetation by fire, and there having been a relative stability in terms of large impacts. The resource patchiness defined concentrated suitable and safe sites for the colonisation by

Table 22: Two-by-two contingency tables from presence-absence data for the spatial association analysis between seedlings of the two species. The observed number of $0.5 m^2$ subplots does not differ from those expected under a random spatial distribution (between brackets) (χ^2-Test, $P<0.05$).

Species	*Austrocedrus chilensis*		Total
Nothofagus dombeyi	present	absent	
present	2 (1.2)	10 (10.8)	12
absent	8 (8.8)	80 (79.2)	88
Total	10	90	100

seedlings, particularly those of *Austrocedrus chilensis* during stand origin, more than a hundred years ago ("inherited site properties", *sensu* Oldeman 1983, 1990). The persistence of a clumped spatial pattern up to the present indicates that selective mortality of the original clumps has not yet taken place at great extent.The shape of age–class frequency distributions has often been used to interpret forest dynamics and impact regimes. However, the interpretation of such age structures is usually inconclusive because their past causes never are known with certitude and great precision. For instance, an even–aged forest identified by using tree age data and therefore assumed to have originated in response to a single massive, extended impact, in fact could be a mosaic of different even–aged tree patches with the range of ages in each patch overlapping, as a response to minor and periodic impacts in the past (Duncan & Stewart 1991). Therefore, to identify even–aged stands or even–aged cohorts within all–aged stands, demographic, physiological or architectural evidence should be analysed together with age data (Lorimer 1985, Oldeman 1990). The "spatial correlation analysis" (Moran 1950) was carried out to test statistically if the patches of trees identified by the Morisita's (1959) indices were of different or of similar ages. Significance tests for autocorrelation coefficient for each distance class (*I*(*l*)) do not provide a test of significance for the data set as a whole, because the *k* (*k*= □*l*) tests are not independent. Therefore, a global test of significance must be performed to verify if *I*(*l*) in at least one distance class is significant at the □/*k* level (Sakai & Oden 1983, Legendre & Fortin 1989). For all distance classes analysed, the spatial correlogram (*z*(*l*) vs. *l*) of *Austrocedrus chilensis* tree ages did not differ significantly from the expected values under random distribution (P<0.05) (figure 19). Therefore, for this species it was evident that no patchiness of tree ages was present in the study plot. In view of this result, the sample site can be more accurately interpreted as occupied by a part of a larger forest eco–unit, "a surface on which at one moment a vegetation development has begun, of which the architecture, eco–physiological functioning and species composition are ordained by one set of trees until the end", with evidence of breaking up of the old, large eco–unit into smaller, younger ones (figure 15) (Oldeman 1990).

Growth and interaction

Table 23: Two-by-two contingency table from presence-absence data for the spatial association of adults between species. The observed number of $25m^2$-subplots does not differ from those expected under a random spatial distribution (between brackets) (χ^2-Test, P<0.05).

Species	*Austrocedrus chilensis*		Total
Nothofagus dombeyi	present	absent	
present	41 (40)	35 (36)	76
absent	68 (69)	56 (55)	124
Total	109	91	200

Rationale

The elementary resources and environmental conditions for plant growth are relatively few and simple. However, growth is extremely influenced by variations and interactions of biological and physical factors and processes operating at both the ecological and the physiological level (Kozlowski & Pallardy 1997b). Differences in productivity amongst plant species and in populations within a species are frequently explained by variations in the genetic constitution of individual plants. Hereditary control affecting growth performance includes biomass partitioning, photosynthesis rates, stomatal conductance, phenology, resistance to stress, and several other traits (Zobel & van Buijtenen 1989, Adams et al. 1992, Rossignol et al. 1998). The individual's genotypic capacity to capture resources is guided by neighbours, their character, number, size, and proximity bringing structure in and filtering what is the same resource pool at the macro–level (Harper 1977, Silvertown & Lovett Doust 1993). In a particular habitat, the growth rate of a plant often is determined by the the limiting factor, which is the least available resource among all resources. An individual plant is stressed by neighbouring plants consuming and reducing the limited resource. This is assumed to be the basic mechanism of a central biotic factor controlling tree and stand growth: resource competition (Bazzaz 1996, Tilman 1997). Competition implies a spatial–temporal process in which biotic and abiotic, and above– and bellow–ground interactions are bound together. Two or more proximal plants of the same or different species compete, simultaneously or not, for resources such as light, nutrients, or water when the supply of one of these elements falls bellow the combined demands of the plants.

Plant competition implies an indirect interaction with resources acting as intermediaries. It consists of two distinct components (Goldberg 1997): an effect that a plant exerts on the abundance of a resource, and a response of the plant to changes in the abundance of this resource. For plants, the strength of competition is frequently measured in terms of the magnitude of growth suppression caused by neighbouring individuals. Individual growth is critically important because it essentially drives the aggregate effects on several other components and properties at different ecological levels (Tilman 1997). For instance, at individual level competition influences the weight, size, number, and form of the organs within a single individual and its architecture, so determining largely its survival probability. Competition

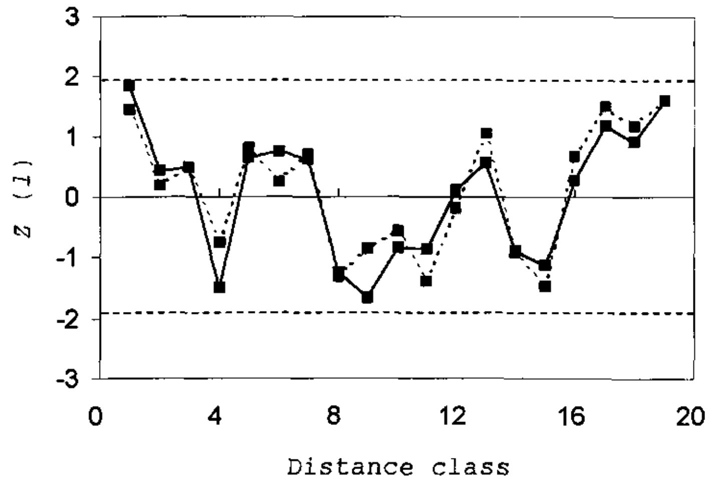


Figure 19: Spatial correlogram of *Austrocedrus chilensis* and *Nothofagus dombeyi* tree ages, for plot A (continuous line) and B (dashed line). *Z(d)* values do not differ significantly from the values expected under random distribution of tree ages, at 0.05 significance level. This probability is indicated with dashed lines.

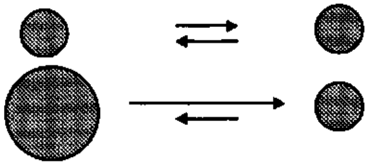
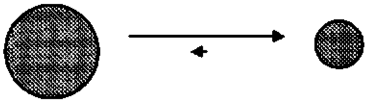
hence influences the density, biomass, size hierarchies, and spatial pattern of a given population.

At community level, the dominance, local or total extinction of species are often at least co–determined by competition. However, upon closer examination this image is askew along the time dimension. The assumption that site properties are practically constant depends on the period considered. No system property is constant over time, neither climate (e.g., El Niño), nor soil (in particular the organic horizon), hydrological structures, or the biotic set of interactions. All ecosystems are filters of abiotic factors, but these filters change every day. One storm thoroughly changes the light climate below the stand by eliminating many twigs and leaves from the canopy (Vester 1997). Change represents stress for some organisms, opportunity for others, which goes further than the above statement by Goldberg (1997). Organisms respond to stress in very precise ways by adjusting or mutating their genomes more or less thoroughly and more or less locally (Rossignol et al. 1998). The result ranges from small adjustment to genetic adaptation and speciation. Hence, the assumption that competing species remain identical over long periods of time also is askew. This means that both the ecosystem as a resource filter, and the species as a finder and consumer of vital resources, show competition as one interaction among many other kinds. For instance, "competition for pollinators" does not exist, because the interaction between pollinator and flowering plant adjusts so rapidly that it optimises this ecological mechanism within the season. Below the ground, the nitrogen budget shows continuous adjustment by tree root symbionts, such as bacteria, mycorrhizal fungi or the microfauna. Roots do not compete for, but adjust to the resource by virtue of their mutualistic interactions. Competition looks quite different depending on the viewpoint. Seen from the side of an individual organism it may look like a potential "danger for itself and its children". Seen from the ecosystem competition is the elimination of a disorderly element that does not fit in, unless it elimination of a disorderly element that does not fit in, unless it adjusts or adapts. Our study concerns individual organisms and Mendelian populations, so the following pages are set in terms of competition.

Two primary competition types can be recognised (table 24). In this distinction, the "symmetrical" type is not to be confused with mutualism, because symmetry does not refer to function but to size. The first type is mainly for resources below the ground, such as nutrients and water. In this case, smaller plants have some adverse effect on the growth of taller plants as well. This kind of competition, also named exploitation, is therefore two–sided. It negatively affects all the interacting individuals and does so in a magnitude relative to their relative sizes. Indeed root systems are able to exploit soil volumes proportional to their own sizes, and hence a resource depletion process inevitably over a number of years affects interacting plants negatively. By contrast, when competition is mainly for light, large plants hinder the growth of smaller neighbours but not *vice versa*. This results in a relative–size asymmetric, one–sided competition, also called interference. There is a resource pre–emption by taller plants, basically for the very large quantitative and qualitative difference between full daylight and light filtered by several layers of leaves (Weiner 1990). One–sided competition has a negative effect on lower competing plants, whereas a neutral response is found in taller plants. These feedback effects increase the variation in growth rates of individual plants and therefore exaggerate relative differences in plant size within a population (Weiner 1990). Nevertheless, the size of light–demanding plants in crowded populations is not usually as great as that plants growing in isolation: plants rarely compete for light without simultaneously competing for subterranean resources, implying that complete asymmetry does not occur (Weiner 1990, Cannell & Grace 1993). Especially in trees, the competition type is susceptible to changes as stand development progresses: for instance, early competition between seedlings is often two–sided, and later on change towards an one–side interaction reflected by an increase in size inequality amongst individuals (Cannell & Grace 1993, also see Oldeman & van Dijk 1991).

Competition comprises a spatial and temporal component. The effect of the "priority of emergence" on size and mortality is indicative of the time component of competition (Silvertown & Lovett Doust 1993). In commerce it would be "first come, first served". The cohorts or individuals that become established earlier in a site attain larger sizes and higher survivorship at a given age than those arriving later, because the former already occupy space and depleted its associated resources (Harper 1977, Silvertown & Lovett Doust 1993, Hutchings 1997). The amount of growth by an individual is more directly determined by its order in the sequence of emergence (the emergence order) than by the actual time at which it emerges (the emergence date): the advantage which an early emerging seedling gains is far greater than the mere effect of the greater time that it has been allowed to grow (Harper 1977). Under one–sided competition, the final outcome is that older, usually larger plants suppress younger, usually smaller plants. The effect of time of emergence on growth is a central issue defining the specific interactions between weeds and crops: the most aggressive weeds are frequently the earliest to emerge (Radosevich & Holt 1984). Distance and spatial arrangement of neighbours also account for large variations in weight and growth of individual plants, reflecting the spatial component of competition. Cannell et al.(1984) showed the effects of close neighbours on the growth of even–aged, monoculture stands of trees. They found that trees taller than all of their closest neighbours exhibited the highest growth rates in diameter, while those with many taller neighbours exhibit

Table 24: Main competition types amongst plants. Note that symmetry refers to the size of organisms, and is not to be confused with functional symmetry like in symbiosis or mutualism.

Type	**Example**
Symmetric: Interference depends on the proportional size of plants. Example: a 100g- plant X reduces the growth of its 50g- neighbour Y two-times the reduction that Y exerts on X. Competition for subterranean resources (- -) (a).	(a) Symmetric 
Asymmetric: Interference is independent of the proportional size of plants. Example: a large plant X reduces the growth of its small neighbour Y. However, Y reduces the growth of X in a very low proportion (competition for subterranean resources) (- -) (b), or there is not inhibition at all (competition for aerial resources) (0 -) (c).	(b) Asymmetric two-sided  (c) Asymmetric one-sided 

the lowest rates. Also, they found an inverse relationship between the probability of a tree dying and the number of its living closest neighbours: trees were more likely to survive if their neighbours had died already. This is primarily a response to one–sided competition for light as larger plants have a more adverse effect on the growth of a smaller plant than *vice versa*.

Although tree growth is susceptible to competition particularly in dense stands, as already discussed, there are substantial divergences in the responses of the diameter and height dimension. Diameter growth tends to follow a negative relationship with crowding: annual rings of subordinate trees are thinner than those of individuals growing rather isolated or in a more advantageous position. Reduction in diameter is caused by late initiation and early cessation of cambial activity, as well as by a decrease in growth rate (Kozlowski & Pallardy 1997a). Changes in spacing of trees, as those following self–thinning, usually determine rapid increases in diameter growth rates of surviving trees. Those trees that become established later usually exhibit very low growth rates in diameter and tend to die first by selective mortality (Peet & Christensen 1987, Oliver & Larson 1996, Smith et al. 1997). Unlike diameter growth, height growth is much less sensitive to the effects of close spacing of trees or of large size, dominant neighbours, and usually small, suppressed trees grow in height at rates that parallel those observed in dominant trees. This is indicative that photosynthate allocation to height growth is given priority over diameter growth (Harper 1977, Oliver & Larson 1996, Barnes et al. 1998).

For instance, during the initial 30 years of a *Pinus strobus* plantation, the first symptom of suppression consisted of a more severe reduction in cambial growth than in height growth in suppressed trees: they made half their total height growth but less than 20% of their total diameter growth (Bormann 1965). Competition for light is claimed to be the primary factor responsible for the evolution of the arboreal life form (King 1990). Although height is rather insensitive to crowding, it is extremely sensitive to the growth resources of a site. This property is often used to evaluate site quality independently of the degree of crowding of the stand, since trees grow in height at approximately the same predictable rate over a wide range of spacing (Waring & Schlesinger 1985, Oliver & Larson 1996).

Results

A summary of stand growth is shown in table 21. Total stem volume growth in plots A and B are estimated to be 6.4 and 8.1m^{3}ha^{-1}yr^{-1}, respectively. Stem dry weight growth in plot A and B is 3.1 and 4.3 t ha^{-1}yr^{-1}, respectively. In plot A, *Austrocedrus chilensis* represents 78.4% of the stand density, although its contribution to stand growth is only 57.0% at a volume basis and 45.2% at a dry weight basis. In plot B, the conifer contributes with 49.6% to total density, but only with 30.4% to growth at volume basis and 22.9% at dry weight basis. These figures indicate the intrinsic lower potential increment of *Austrocedrus chilensis* than *Nothofagus dombeyi*, influenced also by its lower specific wood weight. For the broadleaved species, specific weight is 0.59g cm^{-3}, whereas for the conifer is 0.39 g cm^{-3} (Anonymous 1994). Plot B exhibits a growth rate 27% faster in comparison with plot A. This is primarily attributed to differences in relative stem density between plots of species showing contrasting potential productivity, rather than to differences in site quality.

Comparative data on individual growth rates between species and within development stages are shown in tables 25 and 26. In plot A and B, adults of *Austrocedrus chilensis* exhibit an averaged individual diameter growth rate of 0.36cm yr^{-1}, whereas of *Nothofagus dombeyi* shows 0.57cm yr^{-1}. This represents a growth advantage of the broadleaved over the conifer larger than 58% (table 26, figures 20, 21A). In individual saplings, diameter growth for *Austrocedrus chilensis* and *Nothofagus dombeyi* is 0.11 and 0.21cm yr^{-1}, respectively, representing a growth of the broadleaved exceeding the conifer by over 91% (*t*–Test, $P<0.05$) (table 26, figure 21B). In plot A and B, averaged individual adult height growth was 15.8 and 29.3cm yr^{-1} for *Austrocedrus chilensis* and *Nothofagus dombeyi*, respectively, indicating a difference of morethan 85% in favour of the latter species (table 26). Sapling height growth for *Nothofagus dombeyi* is 17.2cm yr^{-1}, which represents a value 220% larger than that of *Austrocedrus chilensis* estimated to be 7.8cm yr^{-1}. Within development stages, all the increment rates differ significantly between species (*t*–Test, $P<0.05$). These data are indicative of the inherent higher growth capacity of *Nothofagus dombeyi* in comparison with *Austrocedrus chilensis*, regardless the tree size. Between species, the observed difference in sapling growth is of the same order as in adults. However, for both growth variables differences between species are always larger in saplings than in adults: there is a greater growth disadvantage of young conifers facing young broadleaved trees. Growth differences between species tend to decrease in the adult stage (table 26).

Comparative data on individual growth rates within species and between development stages are

Table 25: Summary of tree growth. Mean ($\bar{x}$), standard error (SE), and sample size (N) of diameter (i_d) and height growth rate (i_h) are indicated for adults and saplings of *Austrocedrus chilensis* and *Nothofagus dombeyi*, occurring in plot A and B.

Variable	**Stage**	**Plot**	**Species**								
			$\bar{x}$		SE	N	$\bar{x}$		SE	N	
$\dot{i}_d$ (cm yr^{-1})	Adult	A	0.31	(*)	0.01	152	0.61	(*)	0.03	42	(+)
		B	0.40		0.01	67	0.53		0.03	68	
	Sapling	A	0.11		0.01	20	0.21		0.03	20	(+)
$\dot{i}_h$ (cm yr^{-1})	Adult	A	16.0	(*)	0.3	152	31.3	(ns)	1.3	42	(+)
		B	15.6		0.4	67	27.3		1.0	68	
	Sapling	A	7.8		0.8	20	17.2		2.0	20	(+)

(*) Denotes a significant difference of means between development stages within species (*t*-Test, $P<0.05$). (+) Denotes a significant difference of means between species within development stages (*t*-Test, $P<0.05$). (ns) Denotes a non-significant difference of means between development stages within species (*t*-Test, $P\geq0.05$). Means between plots and within development stages and species do not differ significantly (*t*-Test, $P\geq0.05$).

presented in tables 25 and 26. *Austrocedrus chilensis* adults grow in diameter at rates between 2.8 and 3.6 times significantly faster than their respective saplings (*t*–Test, $P<0.05$). In *Nothofagus dombeyi*, adults grow in diameter at rates between 2.5 and 2.9 times significantly faster than their respective saplings (*t*–Test, $P<0.05$). Within species, diameter growth varies amongst age classes: older trees show significantly higher increments than younger trees (LSD Multiple Range Test, $P<0.05$) (figures 20, 22A, 23). For instance, for *Austrocedrus chilensis* belonging to age classes $1<t<40$ and $t>110$ years, mean individual diameter growth rate is estimated to be 0.07 and 0.40cm yr^{-1}, respectively. For *Nothofagus dombeyi* belonging to age classes 1–40 and 71–80 years, this variable is estimated to be 0.39 and 0.72cm yr^{-1}, respectively. Within species, the large difference in diameter growth between stages and the dependence of diameter growth to age is indicative of the effects of one–sided, asymmetric competition: trees that have arrived to the site earlier had the chances to deplete the resources, to develop larger sizes, and therefore to interfere asymmetrically with those arriving later, according to the rule "first came, first served".

In *Austrocedrus chilensis*, adults grow in height at rates around two times faster than saplings, whereas for *Nothofagus dombeyi* difference in height growth between stages is not significant (table 26). In *Austrocedrus chilensis*, older trees grow in height at significantly higher rates than younger ones (LSD Multiple Range Test, $P<0.05$) (figure 22B). For example, for trees belonging to age classes $1<t<40$ and $t>110$ years, mean individual height growth rate is estimated to be 5.1 and 15.7cm yr^{-1}, respectively. In *Nothofagus dombeyi*, height growth rate is independent of age of individual trees (LSD Multiple Range Test, $P>0.05$) (figures 22B, 24). In this species, trees

Table 26: Comparison of mean diameter (i_d) and height growth rates (i_h) between the species *Austrocedrus chilensis* (*Ac*) and *Nothofagus dombeyi* (*Nd*), and between the development stages adult (AD) and sapling (SP).

Variable	Stages		Species		Species + Stages	
	Adult *Nd/Ac*	Sapling *Nd/Ac*	*A.chilensis* AD/SP	*N.dombeyi* *AD/SP*	AD *Ac*/ SP *Nd*	AD *Nd*/ SP *Ac*
i_d	1.6	1.9	3.2	2.7	1.7	5.5
i_h	1.8	2.2	2.0	–	0.9	3.8

belonging to the age classes $1<t<40$ and $71<t<80$ years exhibit an individual rate of 25.8 and 25.6cm yr^{-1}, respectively. The lower difference between adults and juveniles in height growth in comparison to diameter growth, and the independence between age and height growth for *Nothofagus dombeyi* indicate the priority of height over diameter during development (Bormann 1965, King 1981, 1990, Oliver & Larson 1996, Kozlowsky & Pallardy 1997a). Cross–comparisons involving species and stages are shown in table 26. In diameter, an adult *Austrocedrus chilensis* grows 1.7 times significantly faster than a sapling *Nothofagus dombeyi*. However, an adult *Nothofagus dombeyi* grows 5.5 times significantly faster than a sapling *Austrocedrus chilensis*. In height, an adult *Austrocedrus chilensis* grows at the same rate as a sapling *Nothofagus dombeyi*. On the contrary, an adult *Nothofagus dombeyi* grows 3.8 times significantly faster than a young *Austrocedrus chilensis*.

For adult *Austrocedrus chilensis*, a negative relationship between both individual diameter (R= 0.22 to 0.42cm yr^{-1}) and height growth (R= 11.9 to 20.8cm yr^{-1}), and the number of neighbouring trees taller than itself (0 to 7 or more neighbouring trees within a distance of 5m) is found (LSD Multiple Range Test, $P<0.05$) (figure 25). For individuals of *Nothofagus dombeyi*, although differences in mean values of individual diameter (R= 0.75 to 0.47cm yr^{-1}) and height growth (R= 36.4 to 22.6cm yr^{-1}), in relation to the number of taller neighbours are present, these figures do not differ significantly (LSD Multiple Range Test, $P\geq0.05$) (figure 26). A pattern of variation between individual growth performance and the abundance of taller neighbours is expected when trees are sensible to one–sided competition for, or exposition to light (Cannell & Grace 1993).

Growth and reproduction

Rationale

The completion of a plant's life cycle and the regeneration of a population depends on the production of physiologically independent individuals by reproduction. It involves sexual production of seeds and vegetative production of clones, which have been recently proven by their DNA signatures not to be genetically identical (e.g., Rossignol et al. 1998). In plants, sexual

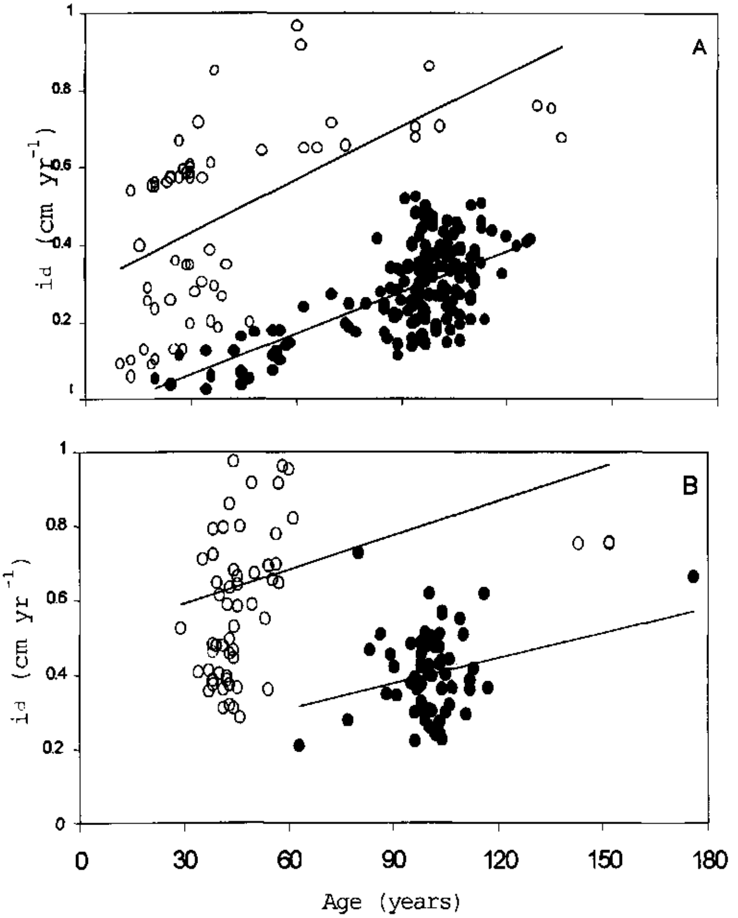


Figure 20: Relationship between mean diameter growth rate (i_d) and age for individuals of *Austrocedrus chilensis* (*Ac*, squares) and *Nothofagus dombeyi* (*Nd*, circles), located in plots A and B. The slope (b) of the equations of simple regression (b_{Ac}= 0.004 and b_{ND}= 0.005) differs significantly from zero (P<0.05) in both species and plots. Sample sizes (N) are indicated in table 25.

reproduction involves great energetic costs in comparison with vegetative propagation. However, short– and long–term benefits presumably outweigh these additional expenditures judging from very the prevalence of sexuality (Maynard Smith 1989). Plant breeding systems are complicated by the occurrence of many sex organs in numerous flowers or cones at any one time. Consequently, there is a much greater sexual variety in plants than in animals (Lloyd 1982). Dioecy or the complete separation of sexes on different individuals, which results in populations that are permanently dimorphic in gender, is rare for most plants groups and for most habitats: about 4% of the total species, mostly occurring in tropical floras, are dioecious, whereas its incidence in temperate trees is very low (Bawa 1980, Lloyd 1982, Crawley 1997b). The vast

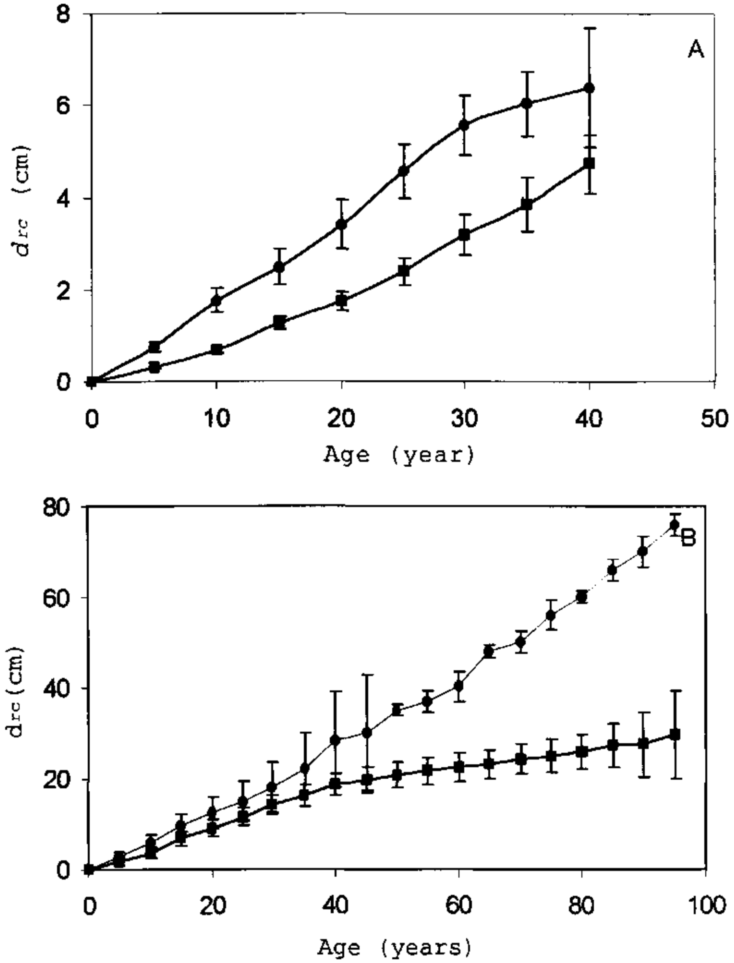


Figure 21: Relationship between root collar diameter (d_{rc}) and age for saplings (A) and adults (B) of *Austrocedrus chilensis* (squares, N= 20 saplings and 239 adults) and *Nothofagus dombeyi* (circles, N=20 saplings and 130 adults). Vertical bars indicate the standard error of the mean.

majority of plants are monoecious with one individual plant supporting male and female flowers They form monomorphic populations, from which around 91% are monocliny, e.g., with hermaphrodite flowers on the same individual, and 5% are dicliny, e.g., with single–sex flowers on the same plant (Crawley 1997b). A very few species of monoecious vascular plants have temporarily separated, environmentally controlled male and female phases (Charnov & Bull 1977). Sexuality almost invariably evolved from monoecious individuals in monomorphic populations to dioecious individuals in dimorphic populations, with an intermediate stage characterised by unisexual mutants in cosexual populations (Bawa 1980, Lloyd 1982). Monoecy facilitates mating, reduces metabolic cost of reproduction basically in animal–pollinated plants,

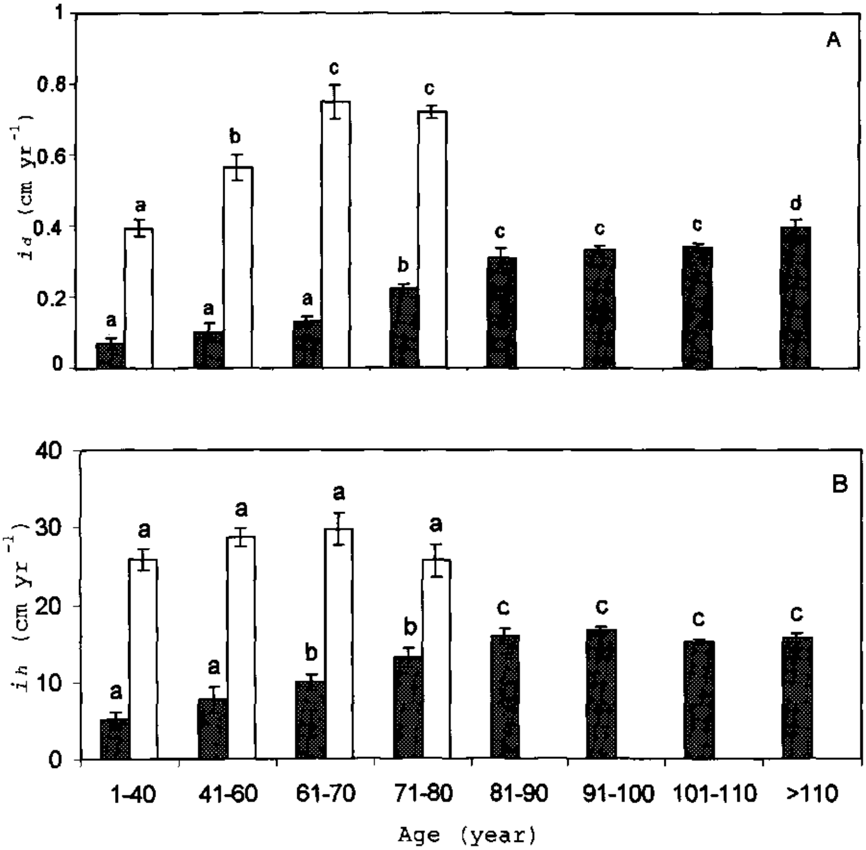


Figure 22: Mean diameter growth rate (i_d) (A) and height growth rate (i_h) (B) related to age for *Austrocedrus chilensis* (shaded bars) and *Nothofagus dombeyi* (empty bars). Different letters (a,b,...,d) indicate significative differences of growth rates within species and between age classes (LSD Multiple Range Test, $P<0.05$). Vertical bars represent the standard error of the mean for a sample size of N= 239 for *Austrocedrus chilensis* and 129 for *Nothofagus dombeyi*.

as the visitor may directly achieve pollination. Moreover, it increases potential fitness by spreading investments over male and female activities rather than relying on one (Lloyd 1982).

Sexuality based on specialised male and female genets may increase reproductive efficiency because the associated costs may be spread over different individuals, it increases genetic variability and heterosis in offspring due to outcrossing, and it enhances fruit production attractive for dispersers (Lloyd 1982). In long–lived, iteroparous perennial plants investment in reproduction does not take place until the requirements for survival, such as growth, storage, and defence have been met (Kozlowski & Pallardy 1997b). Vegetative growth and reproduction are typically bound together by physiological trade–offs, since allocation of limited resources to any one activity will occur at expense of others (Cody 1966, Harper 1977, Newell 1991, Delph &

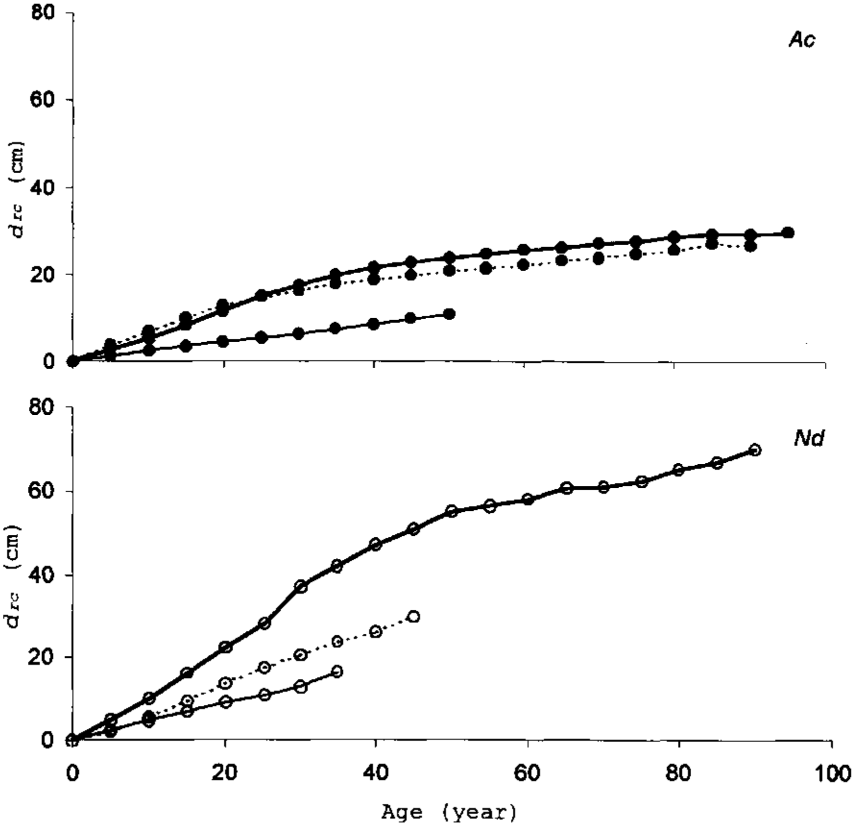


Figure 23: Relationship between root collar diameter (d_{rc}) and age for *Austrocedrus chilensis* (*Ac*) belonging to the age classes 1-70 (continuous thin line), 71-110 (dashed line), and >110 years (continuous thick line), and for *Nothofagus dombeyi* (*Nd*) belonging to the age classes 1-40, (continuous line), 41-60 (dashed line), and >60 years (continuous thick line).

Meagher 1995, Kozlowski & Pallardy 1997b). Reproduction and growth have been identified as the best–confirmed broad phenotypic trade–offs in a review of life history studies by Stearns (1992). This trade–off largely determines the temperament of a forest tree species (Oldeman & van Dijk 1991). In trees, "mast" years of high seed production are marked by very narrow annual rings of wood (Harper 1977, Kozlowski & Pallardy 1997b). Evidence showing the relationship between fecundity and vegetative growth comes from dioecious plants. In dioecious plants, some reproductive functions are shared between male and female plants, such as the production of support organs (e.g., pedicels and peduncles), protective tissues (e.g., bracts and bud scales), attraction signals and rewards substances (e.g., coloured petals, nectar). However, there are other costs inherently linked to either the male or female function. In anthophytes, pure male costs involve the stamens (filaments, anthers, and pollen), and pure female costs the pistil (stigma, style, and ovary) and those associated to seeds and fruits (endosperm, embryo, dispersal structures). The production of seed and fruits represents a major additional resource allocation in

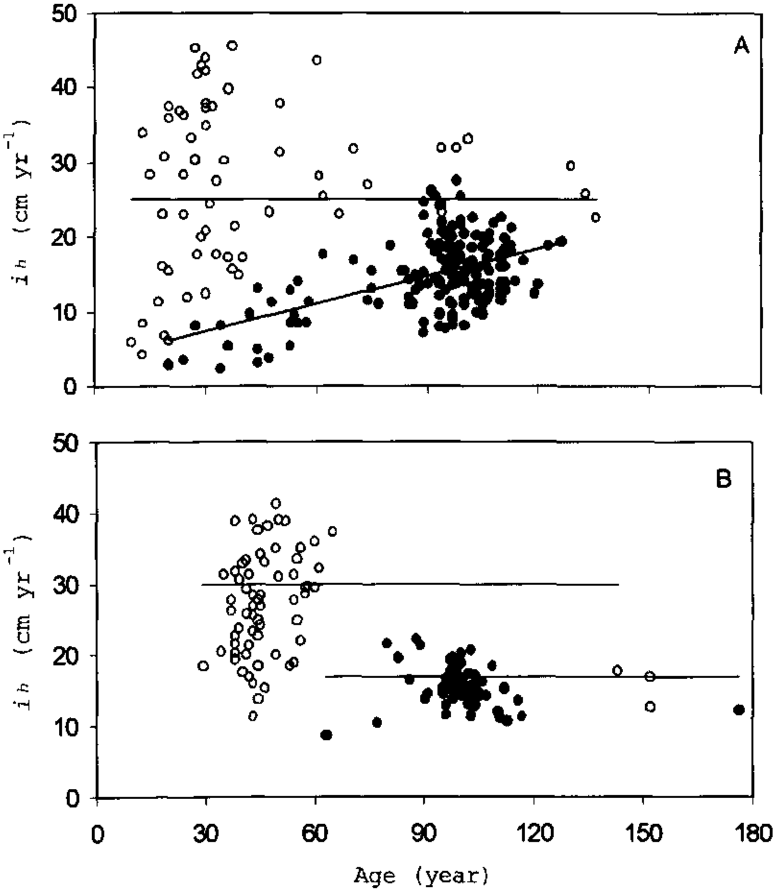


Figure 24: Relationship between height growth rate (i_h) and age for individuals of *Austrocedrus chilensis* (*Ac*, squares) and *Nothofagus dombeyi* (*Nd*, circles), located in plots A and B. The slope (*b*) of the equation of simple regression significantly differs from zero only for *Ac* in plot A (b_{Ac}= 0.001, P<0.05). Sample sizes (N) are indicated in table 25.

females (Lloyd & Webb 1977). Cruden & Lyon (1985) found that most outcrossing plants exhibit greater investment in male than in female reproductive structures for flowers, but after pollination the majority of reproductive biomass is laid down in seeds and fruits. When resources are limited, the seed weight fraction of reproductive biomass tends to decrease because seed production is more expensive than flower production (Bazzaz & Ackerly 1992).

The differential reproductive costs related to gender have been used to explain the presence of different life histories observed in dioecious plants. Relative to males, females have been found to grow slower both during the entire life cycle (Rohmeder 1967, *ex* Harper 1977, Elmqvist et al. 1991, Allen & Antos 1993, Shea et al. 1993), and following a reproductive episode (Agren 1988, Popp & Reinhartz 1988), to exhibit a greater age at first reproduction (Godley 1976, Bullock &

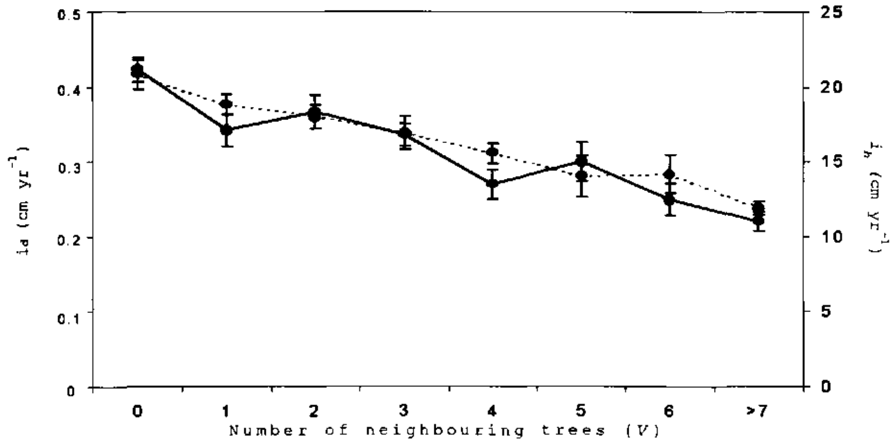


Figure 25: Mean diameter growth rate (i_d, continuous line, primary y-axis) and height growth rate (i_h, dashed line, secondary y-axis) for each *Austrocedrus chilensis* tree (*i*), in relation to the number of neighbour trees (*V*) higher than *i* within a radius of 5m. At least one pair of means differs significantly (ANOVA, $P<0.05$). Vertical bars represent the standard error of the mean of N= 18,14,14,9,18,7,13,and 23 for V= 0,1,...,≥7, respectively.

Bawa 1981), to flower at a later age (Thomas & LaFrankie 1993), and to die at a younger age (Lloyd & Webb 1977, Allen & Antos 1993). In turn, the assumed inferior competitive character and higher mortality of females may determine the existence of male–dominated populations (Rohmeder 1967, *ex* Harper 1977, Lloyd & Webb 1977, Vasiliauskas & Aarssen 1992, Allen & Antos 1993), the microspatial segregation between sexes (Freeman et al. 1976, Dawson & Bliss 1989), and the evolution of sexual dimorphism (Meagher 1992). The preceding examples indicate that the resources involved in reproduction and growth are in fixed supply and that allocation among competing functions is largely mutually exclusive. However, this does not conform to all observations (Bazzaz & Ackerly 1992). Even if phenotypic trade–offs between reproductive and vegetative functions are assumed to be present, in some species females manifest a higher stem and root growth rate, a greater reproductive allocation, and a more extended life cycle than males (Delph & Meagher 1995). This is often accomplished by alternating the timing of allocation to growth and reproduction. Females acquire more resources to invest in carbon–producing structures early in the growing season. This enhances primary productivity, making available more photosynthate for later reproduction without reduction in growth. This is possible by a dip in female metabolic requirements for vegetative growth in the early growing season (Delph et al. 1993).

Results

A striking difference in growth performance was found between sexes in two populations of the dimorphic *Austrocedrus chilensis* forming monospecific stands. In an open woodland (*G*= 20m^{2}ha^{-1}) and in a more dense forest (*G*= 45m^{2}ha^{-1}), males exhibited a mean diameter growth

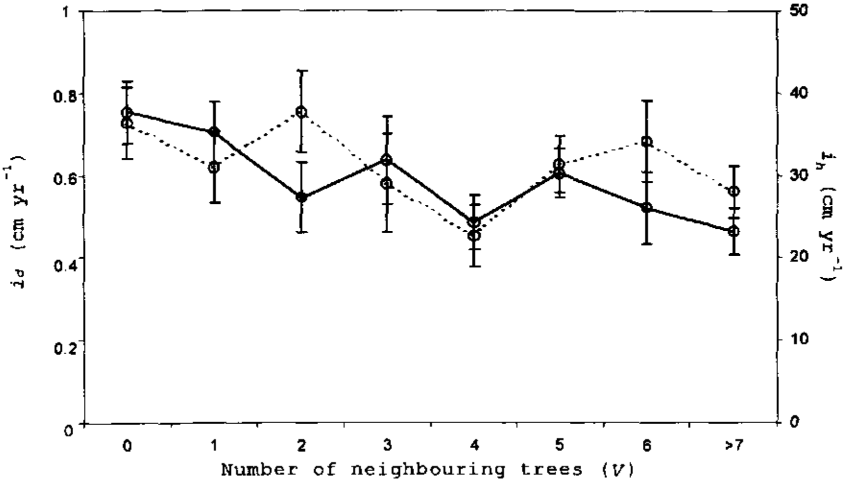


Figure 26: Mean diameter growth rate (i_d, continuous line, primary y-axis) and height growth rate (i_h, dashed line, secondary y-axis) for each *Nothofagus dombeyi* tree (i), in relation to the number of neighbour trees (V) higher than i within a radius of 5m. Means do not differ significantly among them (ANOVA, $P<0.05$). Vertical bars represent the standard error of the mean of N= 4,4,3,2,5,6,3,and 7 for $V= 0,1,\ldots,\geq 7$, respectively.

respectively 77% and 55% significantly greater than females, over the last 22 years of tree life (Sancholuz et al. 1993). These differences were ascribed to contrasting costs of reproduction (Sancholuz et al. 1993). The assumption of a gender–related growth divergence in *Austrocedrus chilensis* is based on the female investment in seeds and fruits, the dissimilar size of the male (smaller) and female (larger) strobilii, and the higher biomass of reproductive structures in females than in males. These features are clear when trees, of equivalent size within a same site, are examined together. However, a comparative quantitative allocation analysis in *Austrocedrus chilensis* has not been carried out, partly because of the difficulties linked to such a studies in long–lived, large–sized species. In the present study, the following hypothesis is re–tested: if in females reproduction involves a greater physiological cost than in males, then their volume growth rate should be lower. Annual wood production was selected as a measure of trade–off because in trees allocation assessment based on biomass underestimates reproductive allocation (Bazzaz & Ackerly 1992). This is due to the continuous accumulation of standing biomass in trees, resulting in a low ratio productivity / biomass. For instance, in the dioecious forests in eastern U.S.A. reproductive structures of trees represented only 0.03% of standing biomass but comprised 1.9% of annual production (Whittaker 1966).

Radial and height growth rates were compared in male and female trees within a population exhibiting a larger basal area than those previously reported (plot A, $G= 67.8\text{m}^2\text{ha}^{-1}$). Individual age in males and females followed a normal frequency distribution (Kolmogorov–Smirnov Test, $P<0.05$). Males on the average are older than females, although the difference is not statistically significant (*t*–Test, $P<0.05$) (table 27). The frequency of diameter and height growth rates

Table 27: Summary on growth in relation to sex class for *Austrocedrus chilensis*. Average ($\bar{x}$), standard error (SE), and range (R) of the variables age, mean diameter growth rate (i_d), periodic diameter growth rate (i_{d22}), and mean height growth rate (i_h). Means do not significantly differ between sex classes (*t*-Test, P≥0.05). Sample size N= 41 males and 39 females.

Variable	Sex class					
	Males			Females		
	$\bar{x}$	SE	R	$\bar{x}$	SE	R
Age (yr)	102.1	1.2	37.0	101.4	1.3	36.0
i_d (cm yr^{-1})	0.13	0.01	0.24	0.12	0.01	0.21
i_{d22} (cm yr^{-1})	0.36	0.01	0.32	0.35	0.01	0.28
i_h (cm yr^{-1})	17.6	0.6	15.3	17.2	0.6	16.4

followed a normal distribution in male and female individuals (Kolmogorov–Smirnov Test, P<0.05) (figure 27). In males and females, mean individual diameter growth rate (i_d) is estimated to be 0.360 and 0.348cm yr^{-1}, respectively. These values do not differ significantly (*t*–Test, P<0.05) (table 27). Periodic individual diameter growth rate (i_{d22}) is estimated to be 0.132 for males and 0.124cm yr^{-1} for females, respectively; these figures do not differ significantly (*t*–Test, P<0.05) (table 27). The cumulative diameter for *Austrocedrus chilensis* males and females, calculated for five–year intervals, follows an equivalent trajectory indicating no contrast between sexes (figure 28). In males and females, mean individual height growth rate (i_h) is estimated to be 17.6 and 17.2cm yr^{-1}, respectively, a values that do not differ significantly (*t*–Test, P<0.05) (table 27).

Stand dynamics

An aggregation of trees of a single–age class proceeds from birth to death through a continuous process. For analytic purposes, this sequence has been divided in phases constituting the forest development cycle (Bormann & Likens 1979, Oliver 1981, Peet & Christensen 1987, Oldeman 1990). For temperate forests, Oliver (1981) has proposed a model of stand development in four phases, in which the dynamics are strongly influenced by periodic major impacts as the starting point for the rejuvenation of vegetation. The first phase at the beginning of secondary succession is designated "stand initiation stage". It is characterised by tree establishment after massive impacts open up a growing space. In this site, development starts from the propagule bank with its seeds, spores, and cuttings, by surviving advance regeneration of local origin, or by propagules from distant sources (Oldeman 1990). The newly opened space is first occupied by herbs showing a short–lived, opportunistic temperament. Sites exhibit a high resource availability, and a high seedling mortality caused by density–independent processes. When the

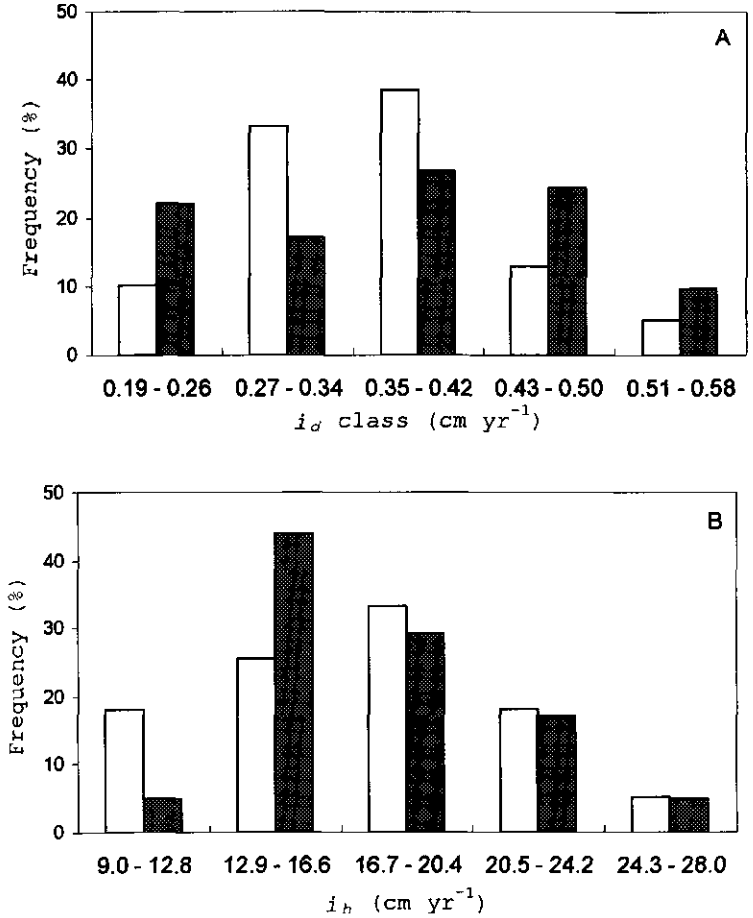


Figure 27: Mean diameter growth rate (i_d)-class frequency distribution (A) and mean height growth rate (i_h)-class frequency distribution (B) for *Austrocedrus chilensis* males (shaded bars, N= 41) and females (empty bars, N= 39).

growing space above and bellow the ground is filled with plants, tree crowns close the horizontal canopy. Canopy closure defines the start of the second phase of the forest development cycle: Oliver's (1981) "stem exclusion stage" or Oldeman's "aggradation phase" (*ex* Bormann & Likens 1979). Trees start to compete with each other. The more vigorous ones survive, the weaker ones are suppressed and often die. Selective mortality, a highly density–dependent, non–random process caused by suppression, determines two main changes at stand level: a decrease in tree density due to mortality, and an increase in biomass by vigorous growth of surviving trees. A size hierarchy with few large–diameter trees, and many trees exhibiting lower diameters usually develops in the stand.

Although establishment of additional regeneration of the same colonising species is infrequent,

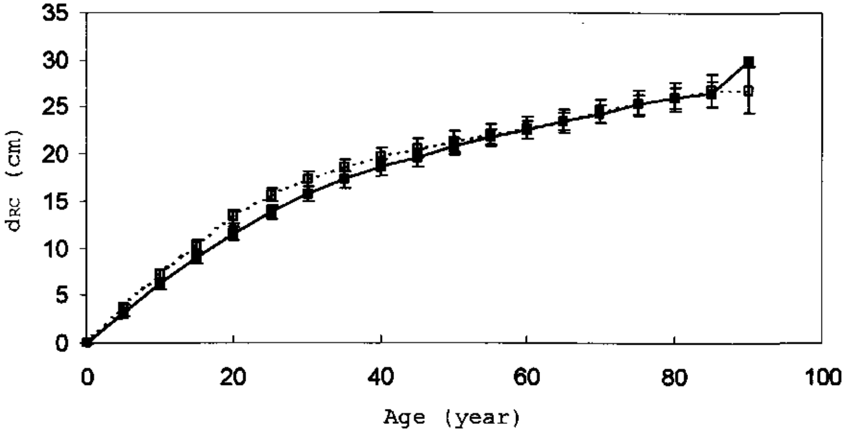


Figure 28: Cumulative diameter (d_{rc}) for *Austrocedrus chilensis* males (shaded squares, continuous line, N= 41) and females (empty squares, dashed line, N= 39), calculated in five-years intervals. Vertical bars indicate the standard error of the mean.

the establishment of shade–tolerant trees may start underneath the main canopy. If during the first development phase the initial density is low and dominated by slow–growing species, self–thinning may be delayed or even skipped. A maturing temperate stand will gradually enter Oliver's (1981) "understorey reinitiation stage". Scattered trees that survived the previous mortality wave begin to die by density–independent mortality associated to ageing and senescence. Gaps then allow the establishment and growth of new plants of diverse origin, e.g., light–demanding trees of the same species as those in the overstorey, or shade–tolerant species differing from those in the canopy and already present as advance regeneration. This transition phase, named the "old–growth stage" (Oliver 1981), is characterised by a death of mature trees and a replacement by younger individuals. This process leads to a silvatic mosaic constituted by patches of even–aged of trees, the birth of which tends to correspond to the opening of the canopy gaps. In each of the patches, the complete cycle is expected to take place again, but at a smaller spatial scale. This conceptual model has been used to explain the development pathway following secondary succession in the *Nothofagus* forests located in southern South America and elsewhere (e.g., Veblen et al. 1996).

From 1911 to 1913, Willis (1914) travelled in northwestern Patagonia and mapped in detail the natural vegetation and the land–use patterns in different areas of this region. This is the first scientific publication on the geology and vegetation of the region. One of the mapped areas corresponds to the location of the sample stand (figure 29). At that time, the study site was dominated by shrubs and low trees, surrounded by virgin forests of *Nothofagus dombeyi* and *Austrocedrus chilensis*, interspersed with recently burned areas (Willis 1914). The vegetation in the study site indicated an earlier forest burning, and there was livestock grazing (Willis 1914). This activity presumably was discontinued soon after, because a recent study on human influences does not place the stand in a zone of historical grazing (APN 1986). The observations by Willis (1914) and our estimates of tree ages, show that the burning of the original community and the origin of the current stand are not related to the phase of huge forest fires that

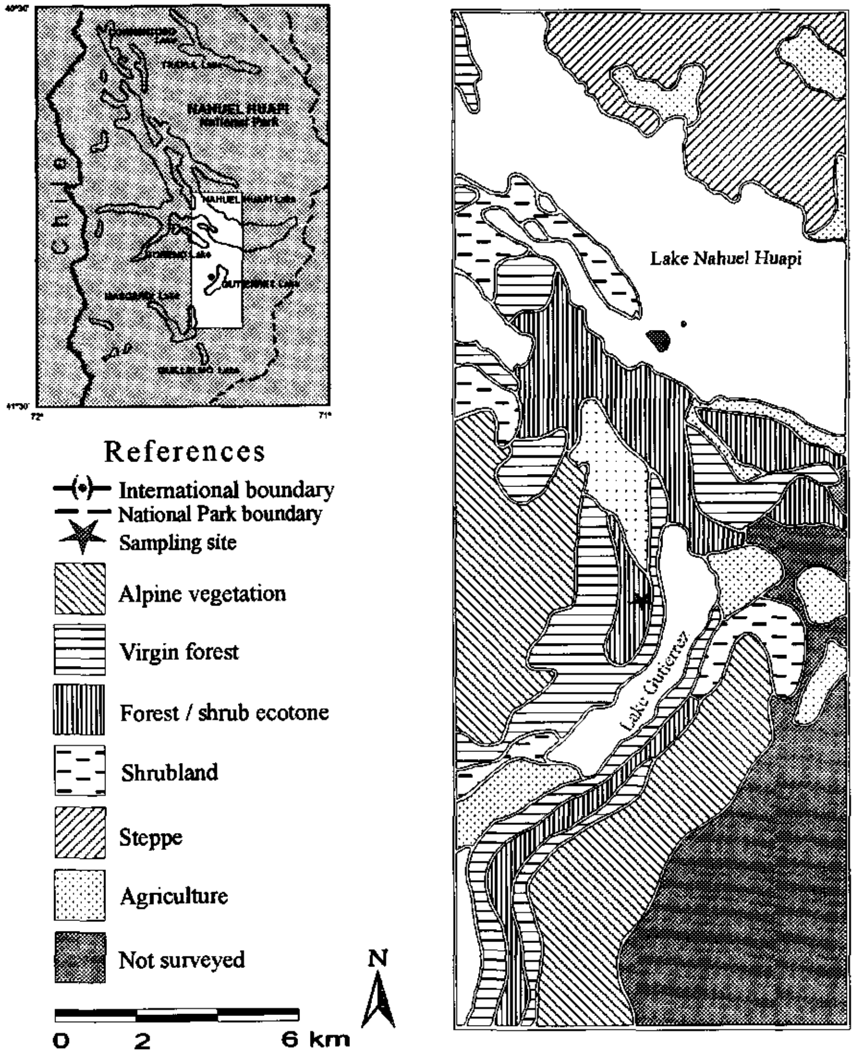


Figure 29: Location of the sampling site and the vegetation and human activities in the area at the beginning of the twentieth century (Willis 1914).For general position see maps of southern South America (figure 1) and western Patagonia (figure 6).

characterised the period of European colonisation between 1880 and 1930. In the area, colonisation by *Austrocedrus chilensis* and *Nothofagus dombeyi* began around 1860 (table 21, figure 13). Therefore, the forest fire should be dated before this time when others inhabitants were present in the region. The fires may have been lighted naturally or by people. For example, Rothkugel (1916) attributed the origin of an even–aged *Nothofagus dombeyi* stand of 150 years to burning by Jesuits or Indians to create pasture lands in the seventeenth century. Veblen &

Lorenz (1987) also claimed that the origin of many *Nothofagus dombeyi* and *Austrocedrus chilensis* stands preceded European settlement.

The original community was completely removed by this fire. A period dominated by shrubs, which grew and spread rapidly probably characterised the area during the first stage of secondary succession. Around 130 years ago, trees began to colonise the area. This was the initial regenerative pulse of which traces remain in the stand. The period of successful coniferous recruitment appears to have been highly synchronous in the study site, which indicates a response to the same event or process. Individuals became established in a clustered spatial pattern (figures 13, 17, 18), presumably in response to a local environmental heterogeneity, "the abiotic and biotic remanence" of Oldeman (1990). At the beginning of the "stand initiation stage" (*sensu* Oliver 1981), trees had overtopped and replaced the shrub vegetation. *Austrocedrus chilensis* was more successful than *Nothofagus dombeyi* judging from the clear differences in the respective abundance of adult trees: in both plots, there is a marked scarcity of adult *Nothofagus dombeyi* whereas *Austrocedrus chilensis* is well represented (figure 13). The inherent ability of the drought–tolerant *Austrocedrus chilensis* to become established and grow on the burnt out, exposed to the north site, with an expected higher irradiance and evaporative stress, accounts for its initial high density. The more moisture–demanding *Nothofagus dombeyi* experienced high mortality by desiccation on this drier slope. Individuals of *Nothofagus dombeyi* that survived this presumably critical period, constitute the biggest and higher trees of the stand (figures 14, 15), due to their faster growth rates (tables 25, 26). Few trees may have survived the original impact, as reflected by the presence of relatively old and isolated trees of both species, with extensive fire scars in their trunks.

During the "stand initiation stage" that lasted between 60 to 70 years, a single even–aged cohort emerged in the *Austrocedrus chilensis* tree population (figure 13). The *Nothofagus dombeyi* population is poorly represented within this cohort in both plots (figure 13), although a normal distribution of ages is also observed in plot A. In young forests originating after major impacts, a normal age curve is usually found in light–demanding species exhibiting a "catastrophic" regeneration mode. This results from the exclusion of new trees as long as the canopy is closed, because regenerative requirements are not met (Oliver 1981, Lorimer 1985). The relatively long duration of this forest development phase is explained by the slow growth of the initial invading trees, whence their inability to rapidly exclude later arrivals. Highly platykurtic and symmetrical age distributions are common after large–scale impacts, where site conditions and species characteristics promote slow growth patterns (Oliver & Larson 1990). Oldeman (1990) speaks of blocked forest development.

Within the stand, the next development phase that left its traces is the "understorey reinitiation stage" (*sensu* Oliver 1981). It began around seventy years ago with the onset the establishment of an understorey cohort principally constituted by *Nothofagus dombeyi* saplings, and defining a second regenerative pulse (figure 13). After canopy closure, regeneration resumed over a period particularly important for the broadleaved species. The humidity of the site that was probably too low for earlier colonisation by the mesic *Nothofagus dombeyi* increased, and so the species could them develop a large uneven–aged understorey. On the contrary, regeneration of *Austrocedrus chilensis* beneath the canopy was failing, as proven by the comparatively low sapling density, its bell–shaped age distribution in plot A (figure 13A), and its almost complete absence within the age classes $20<t<60$ years in plot B (figure 13B). *Nothofagus dombeyi* exhibits a pattern of rather continuous regeneration as shown in the *L*–shaped age class distribution of the understorey cohort. This suggests that this species is also capable to colonise small gaps under certain site conditions as also suggested by Veblen et al.(1981) and Veblen (1989). Probably, the lack of shade–tolerant trees and the scarcity of the tall bamboo *Chusquea culeou*, has allowed *Nothofagus dombeyi* to germinate and growth more continuously. A third regenerative pulse is represented by a large cohort of seedlings and saplings dominated in abundance by *Nothofagus dombeyi*, which is supposed to be highly unstable as a results of large likelihood of mortality given the suboptimal conditions in relation to light. Similar patterns were found in several variations in the northern mixed *Fagus* forests (Peters 1997).

At present, the stand shows structural features of different phases of forest development. The persistence of a clumped spatial structure in both species populations (figures 17, 18), and the "*L*–shaped" size structure in the *Nothofagus dombeyi* population (figure 12) demonstrate the near–absence of selective mortality and of the smallest individuals. These structures are characteristic of stands at the initiation of the second phase of forest development, e.g., the "stem exclusion stage" *sensu* Oliver (1981) (Mohler et al. 1978, Peet & Christensen 1987), or the "natural forest fragmentation" (*sensu* Oldeman 1990). The recent development of a new cohort, and its growing size due to the increasing rate of recruitment of *Nothofagus dombeyi* saplings (figure 17), shows that the stand is in the "understorey reinitiation stage" now. As pointed out by Peet & Christensen (1987), if stocking of new trees is slow during stand initiation, the onset of selective mortality is delayed. For this reason the stand must have bypassed the second phase, so going directly to the "understorey reinitiation stage". However, selective mortality may still take place later. The abundance of young saplings of each species is not positively correlated to that of old adults of the same species. If a stand is in compositional equilibrium, the number of trees belonging to those development stages of trees should be proportional. A negative correlation between these numbers and phases indicates compensatory recruitment of sub–dominant species and increased probability of a shift in dominance within the stand (Connell et al. 1984). Gaps created by fall of senescent adult trees will allow the emergence of advance regeneration or new germination of *Nothofagus dombeyi*. The saplings of *Austrocedrus chilensis* are possibly unable to compete with them, given their lower numbers and lower growth rates (tables 21, 25, 26). A series of eco–unit mosaics, made by the gaps opened up by treefall and dominated by *Nothofagus dombeyi*, is expected to occur. The occurrence of periodic allogenic, large–scale impact differentially favours site re–colonisation by *Austrocedrus chilensis*, whereas the absence of such events favours a larger colonisation by *Nothofagus dombeyi*. However, the great longevity of *Austrocedrus chilensis* (a "long–lived pioneer", see Oldeman & van Dijk 1991) implies that its successional displacement can bridge the absence of stand–level impacts for periods up to 500 years. In future development of the forest, the capacity of *Austrocedrus chilensis* to persist underneath the canopy will also be decisive: if it can grow as a sub–dominant tree tolerating shade, as shown in other studies on mixed forest (Veblen & Lorenz 1987, Veblen 1989), it is probable that only a shift in dominance will occur. If not, *Austrocedrus chilensis* may become successionally replaced. Any new large–scale impact interrupts these development dynamics, reinitiating the secondary succession towards an even–aged *Austrocedrus chilensis*–dominated mixed forest.

Minimum area

Rationale

Vegetation science comprises the study of spatial and temporal patterns of plant populations, communities, and major units of aggregation (Wiegleb 1989, Glavac et al. 1992). The description, explanation, and prediction of those patterns is mostly based on observation and induction (Greig–Smith 1983). Vegetation is analysed by using different sampling techniques and designs, based on the examination of a sample or a portion assumed to be representative for the whole. Sampling involves a decision–making process regarding the selection of the study area, the relevant physical and biological variables, and the type (e.g., sampling with or without delimited plots), location (e.g., randomly or regular), shape (e.g., circular or rectangular), and size of the sampling units (Mueller–Dombois & Ellenberg 1974). The final sampling set–up results from a balance amongst the specific objectives, the vegetation features, and the availability of resources. In quantitative plant ecology, a methodological key issue concerns the selection of the appropriate size of the sampling area, either based on a plot–less (e.g., Cottam & Curtis 1956) or on a plot–delimited approach. This apparent trivial question has generated strong controversies since the end of the nineteenth century (Goodall 1961). Failures to standardise the size of the study area and many other practical considerations have led to a great divergence in experimental approaches, frequently causing great difficulties in comparing the findings of different studies (Crawley 1997c). The statistically optimum plot size for the analysis of structural attributes of vegetation varies according to the biological properties of the community (species composition, abundance, spatial pattern of individuals), the variation of size and growth amongst individuals, and the required level for estimate accuracy (Lorimer 1985). Therefore, the plot size should be empirically ascertained in each particular case. However, the optimal areas recommended by different authors, mostly following vegetation–type analogies, are often used as a recipe for such reasons as mere lack of resources and time.

Based on the concept of "minimum area of the community" (MA), the phytosociological school of Zürich–Montpellier developed two quantitative methods to estimate the optimum plot size. Such analytical approaches are used not only for plant community delimitation based on species composition (syntaxonomy), but also for ecological studies on the interactions amongst organisms and their environment. The first method determines the smallest area in which the species composition of a given community is properly represented. A bi–dimensional diagram is constructed from species counts occurring in successive plots of increasing size, usually nested, resulting in a "species (S) – area (A)" curve. This MA (or "qualitative MA" *sensu* Meijer Drees 1954, *ex* Barkman 1989) represents the smallest tract in which the cumulative number of species reaches a certain stability, likely to include some asymptotic percentage of the total flora of the community (Cain 1938, Vestal 1949, Moravec 1973).

The previous definition assumes that communities exhibit a fixed total flora and an unique relation between species richness and area. However, these two assumptions were proved not to be universally valid. Firstly, increasing square size usually conducts to increasing species number. This is reflected in the fact that S and A are frequently related by a logarithmic function of the type $S = k + z \log A$, with k and z being empirical constants (Hopkins 1955, Dahl 1960, Ashton 1965, Kilburn 1966, Dony 1977, Barkman 1989). Both also are often related by a power functions of the type $S = k\ Az$ (Archivald 1949, Kilburn 1966, Dony 1977, Loehle 1990). There are many practical difficulties to determine MA from S–A curves, simply because the saturation of species number is never attained in both models. There are also scale problems in accounting for organisms widely differing in size, such as large trees and small herbs (e.g., see van Rompaey 1993). Secondly, measurement of richness based on frequency counting depends on the spatial patterns of species distribution. Hence, a MA analysis presupposes a knowledge of both the degree of aggregation of species, and the extent of correlation between the spatial patterns of those species (Crawley 1997c). For instance, for a high equable community, e.g., all species being equally abundant with randomly dispersed individuals in a "fine–grained" pattern, the *S–A* curve follows the classic asymptotic form. However, if several equally abundant species formed by dense, non–overlapping clustered populations, in a "coarse–grained" pattern, the *S–A* curve increases following a linear step–wise manner (Oldeman 1978, Crawley 1997c). An alternative approach analyses the size of an area above which the quantitative participation of the species (e.g., in cover or biomass) does not significantly change. Variation in mean and variance of selected variables are examined in relation to different block sizes. Each block size is obtained by the progressive combination of sampling units or subplots. This MA (or "quantitative MA" *sensu* Meijer Drees 1954, *ex* Barkman 1989) represents the block size in which the variance becomes stabilised or eventually equals 0 (Greig–Smith 1952, Bormann 1953, Mangenot 1955, *ex* Oldeman 1990, Goodall 1961,1974, Kershaw 1973, Usher 1975, Dietvorst et al. 1982). This procedure is preferable because involves the consideration of the species present and their abundance (Goodall 1961, Barkman 1989).

Results

Based on the concept of the "quantitative minimum area", the statistically optimum plot size for the study of this mixed, evergreen, even–aged temperate stand is determined. The findings are compared with those in literature and are presented as a possible reference for future studies on the ecology and management of the Patagonian forests. The analysed variables comprise the contribution of adult trees of both species, expressed at subplot basis. Values of density (D), basal area (G), volume (V), and volumetric growth (I_v) exhibit a great variation within a range of small block sizes, but they become quite stable from a sampling area larger than 1,000m^2 on (figure 30). The accuracy level of the estimates of D, G, V, and I_v, measured as the relative error RE (eq.5.23), increases as long as the block size is expanded (figures 30, 31). However, RE, which reflects differences between content of blocks, varies exponentially with block size: within a range of small block size RE decreases rapidly, but as the sampling area increases RE diminishes more slowly (table 28, figure 31). Furthermore, RE exhibits large values in all the range of block size analysed (figures 30, 31). For instance, for a sampling area of 1,000m^2, D= 1.6ind SP^{-1}± 30%, G= 0.23m2SP^{-1}± 40%, V= 1.8m^{3}SP^{-1} ± 49%, and I_v = 0.02m^{3}SP^{-1}yr^{-1} ± 39%. For a sampling area of 2,500m^2, D= 1.5ind SP^{-1} ± 20%, G= 0.18m^{2}SP^{-1} ± 25%, V=1.4m^{3}SP^{-1} ± 32%, and I_v = 0.02m^{3}SP^{-1}yr^{-1} ± 23%. An area of 5,600m^2 is necessary to establish for sampling to obtain a RE= ±20%, according to regression equations developed between RE and all the structural variables examined (table 28).

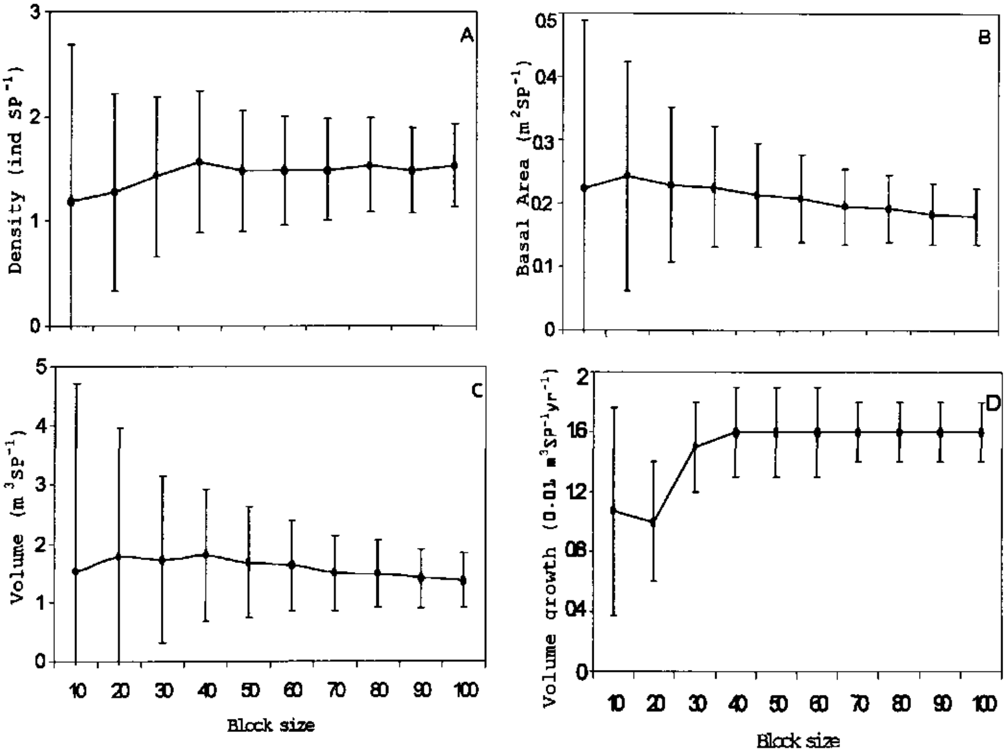


Figure 30: Mean and 95% confidence interval of the tree density (A), basal area (B), volume (C), and volume growth rate (D), in relation to block size. Each block size represents the number of 5x5m subplots utilised for the estimation of the variables.

Table 28: Intercept (a) and slope (b) of the simple regression equation ($RE= aX^b$, $P<0.05$) between the relative error (RE (%) = 100 ($t\ s_{\bar{x}} / \bar{x}$)) of the estimated density (RE_N), basal area (RE_G), volume (RE_V), and volume growth rate (REI_V), in relation to block size (X). Each block size represents the number of 5x5m subplots utilised for the estimation of the variables. Regression coefficient (R^2), sample size (N), and the required area to obtain RE= ±20% (A, in m^2) is also indicated.

RE (%)	a	b	N	R^2	A
REN	239.1	-0.54	10	0.991	2,495
REG	407.6	-0.61	10	0.997	3,500
REV	333.8	-0.52	10	0.992	5,600
REI_v	426.4	-0.64	10	0.976	2,980

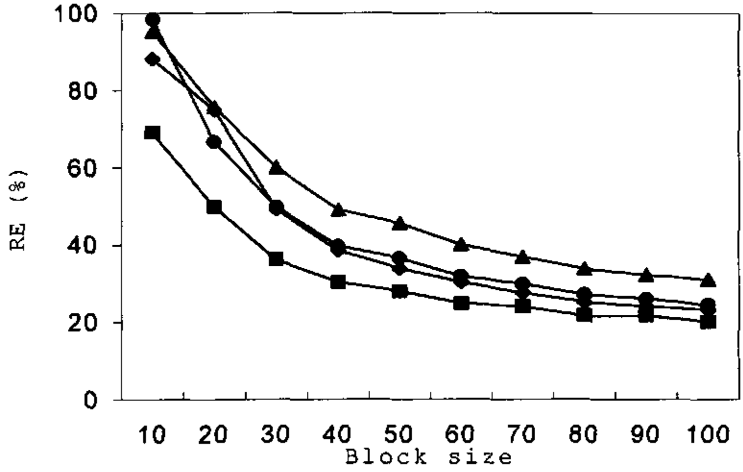


Figure 31: Relative error RE (RE (%) = 100 (t $s_{\bar{x}}$ / $\bar{x}$)) of the estimated tree density (*D*, squares), basal area (*G*, circles), volume (*V*, triangles), and volume growth rate (I_V, rhomboids) per subplot, in relation to block size. Each block size represents the number of 5x5m subplots utilised for the estimation of variables.

6. CONCLUSIONS

> "In conclusion, it seems clear that forestry is ultimately a branch of ecology and will advance as a discipline only as swiftly as ecology advances. Progress in both domains will depend in good part on the study of biodiversity; the variety of life in the infrastructure of forests is immense, fragile, and still very poorly understood. Finally, the two disciplines are bonded in another way: biodiversity is vital to healthy forests, while proper management is vital to the maintenance of biodiversity."
>
> Edward O.Wilson (1993).

Stand and tree growth

As an adult tree, *Austrocedrus chilensis* exhibits an inherently lower growth capacity in height and diameter than its neighbour *Nothofagus dombeyi*. The intrinsic capacity of *Nothofagus dombeyi* to grow in diameter at faster rates than *Austrocedrus chilensis* has been observed previously (Veblen & Lorenz 1987, Anonymous 1994) (table 29). This differential growth performance can be explained by divergences in net photosynthetic rates: *Nothofagus dombeyi* exhibits a more efficient net photosynthesis based on both leaf area (NAR) and individual (i_b, i_v) (Anonymous 1994) (table 29). This higher assimilation rate compensates its lower allocation to leaves (LAI, b_l) (table 29). The life span of leaves seems not to differ largely: for *Austrocedrus chilensis* needle longevity is estimated to be four years (Anonymous 1994), whereas *Nothofagus dombeyi* leaves live during three years (Anonymous 1994) or four (Hevia et al. 1999). When compared to the southern beech, *Austrocedrus chilensis* trees show a lower difference in radial and height growth during the adult than in the juvenile stage, probably as a result of contrasts in relative photosynthetic mass between development phases. There is ample evidence that seedling represents the intrinsically slowest growing ontogenetic phase in gymnosperms, caused by multiple factors related to leaf productivity and allocation. This characteristic has been applied to explain the decline and retreat of this plant group occurring along evolutive scales. *Nothofagus dombeyi* exhibits one of the highest potential growth rates observed within the genus. In Great Britain, in plantations growing under optimal conditions it reaches a mean diameter of 94cm in 50 years, whereas at the same age *Nothofagus obliqua*, *Nothofagus nervosa*, and *Nothofagus antarctica* attain 68, 72, and 46cm, respectively (data from Tuley 1980) (figure 32). In two-year old seedlings, *Nothofagus dombeyi* exhibited the highest instantaneous light compensation point and chlorophyll concentration in comparison with other *Nothofagus* species (Read & Hill 1985) (figure 33). High values of these variables are indeed expected in light–demanding species showing rapid growth rates. Perhaps deciduous angiosperms, admitting more light in their understorey during part of the year, were selection factors in the evolution of faster–growing northern conifers (Hallé et al. 1978).

As in *Austrocedrus chilensis*, southern hemisphere conifers show a low productivity when growing in stands with broadleaved species, probably because they cannot benefit from an extended period of net photosynthesis as they co–exist mainly with evergreen species (Enright &

Table 29: Physical and growth characteristics of *Austrocedrus chilensis* and *Nothofagus dombeyi* adult trees. Mean values of individuals in even-aged populations conforming a single-cohort stand are shown. b_L= leaf dry-weight biomass, b_T= total dry-weight biomass, LAI= leaf area index, LP= leaf production, NAR= net assimilation rate, i_V= stemwood volumetric growth rate, i_b= stemwood dry-weight growth rate, and SLA= specific leaf area (Anonymous 1994).

Variable	*Austrocedrus chilensis*	*Nothofagus dombeyi*
b_L (Mg)	0.02	0.01
b_T (Mg)	0.33	0.41
LAI (m^2m^{-2})	2.9	1.6
SLA (cm^2mg^{-1})	0.06	0.08
LAR (m^2Mg^{-1})	307.2	252.9
LP (kg yr^{-1})	7.4	8.1
NAR (kg m^2yr^{-1})	0.12	0.21
i_b (Mg yr^{-1})	0.01	0.02
i_V (dm^3yr^{-1})	7.3	19.6

Odgen 1995). However, conifers from the northern hemisphere tend to show a yearly primary productivity similar to their associated primary deciduous angiosperms, as discussed previously. Norton et al.(1987) have summarised growth data from New Zealand tree species comprising the genera *Agathis* (Araucariaceae) (1 species), *Beilschmiedia* (Lauraceae) (2), *Phyllocladus* (2), *Prumnopitys* (2), *Dacrydium* (1), *Halocarpus* (1), *Lagarostrobos* (Podocarpaceae) (1), *Libocedrus* (1), and *Nothofagus* (2). They reported individual annual growth rates in radius of 1.08mm ± 0.19 (mean ± SD) for angiosperms and 0.75mm ± 0.30 for gymnosperms. For angiosperm and gymnosperm trees, Odgen et al.(1993) reported 1.48mm ± 0.63 and 0.98mm ± 0.34, respectively. Lusk & Odgen (1992) calculated an individual annual rate of 1.55mm ± 0.08 for angiosperm trees, including *Elaeocarpus dentatus* (Elaeocarpaceae), *Nestegis cunninghamii* (Oleaceae) and *Weimannia racemosa*, against 1.07mm ± 0.05 for individual gymnosperm trees including *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *Prumnopitys taxifolia*. These figures represent mean growth rates of broadleaved trees superior by 50% over their co-occurring conifers. Growth capacity in native conifers from southern South America is within the range indicated for other conifers of the southern hemisphere. *Pilgerodendron uviferum* (Cupressaceae) shows an individual radial growth between 0.51 and 0.74mm yr^{-1} (Young 1972, *ex* Roig et al. 1992, Roig et al. 1992), and *Fitzroya cupressoides* has a mean individual radial growth rate inferior to 1mm yr^{-1} (Kalela 1941, Lara 1991). *Austrocedrus chilensis* shows a growth lag that is larger during the juvenile than in the adult stage. This pattern is observed in gymnosperms as a group regardless of the geographic distribution.

The increment of younger and smaller *Austrocedrus chilensis* is lower than in older and larger ones. Furthermore, there is a negative relationship between individual growth rate and the number of taller neighbouring trees. *Nothofagus dombeyi* trees also show the lowest diameter increment in the young age classes. However, the individual growth rate in height is independent of the individual age of trees and of the number of taller neighbours within a given distance.

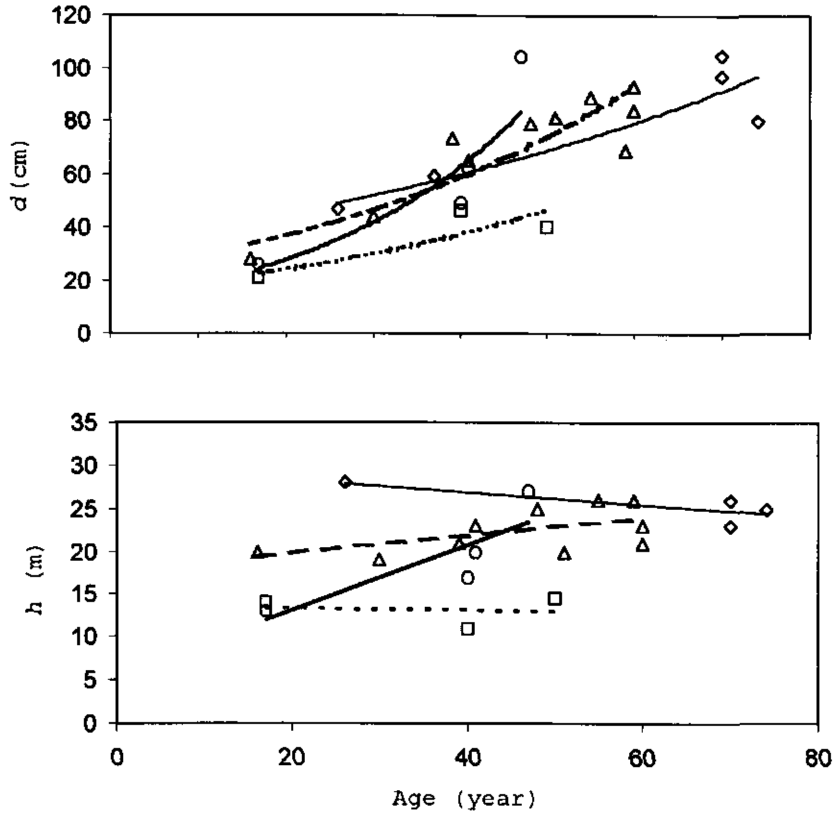


Figure 32: Example of the largest individuals of different *Nothofagus* species, growing under optimal conditions in the British Isles. Allometric relationships between diameter at breast height (*d*), height (*h*), and age for *Nothofagus antarctica* (squares, dotted line), *Nothofagus dombeyi* (circles, continuous broad line), *Nothofagus nervosa* (triangles, broken line), and *Nothofagus obliqua* (rhomboids, continuous fine line) are shown. The genus was introduced in Britain in 1849. Data from Tuley (1980).

For *Nothofagus dombeyi*, the intercept (*a*) and the slope (*b*) of the exponential equation of regression ($d = e^{a+b\,Age}$) is 2.49 and 0.04, respectively (R^2= 0.883, N= 4); for *Nothofagus obliqua*, *a*= 3.52 and *b*= 0.01 (R^2= 0.886, N= 5); for *Nothofagus nervosa*, *a*= 3.13 and *b*= 0.02 (R^2= 0.831, N= 10); for *Nothofagus antarctica*, *a*= 2.73 and *b*= 0.02 (R^2= 0.797, N= 3).

Hence, *Austrocedrus chilensis* must either die or survive the stress of suppression by old and firstly emerging trees. On the contrary, its neighbour *Nothofagus dombeyi*, with its insensitivity of both growth variables to crowding, and its height growth indifferent to the effect of older and larger trees, would exhibit a higher chance of survivorship and emergence. Indeed, stemwood production is linearly related to the amount of intercepted radiation, and this relation is largely unaffected by water and nutrient shortages. Plants under stress produce a reduced leaf area,

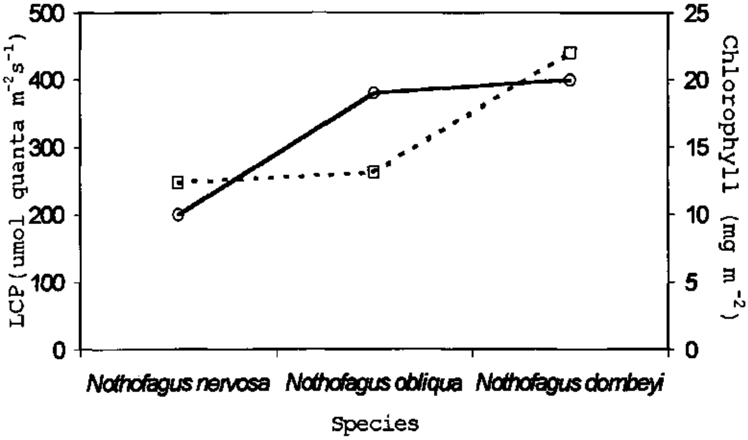


Figure 33: Light compensation point (LCP, continuous line) and chlorophyll content (dashed line) of two-year old *Nothofagus dombeyi*, *Nothofagus nervosa*, and *Nothofagus obliqua* seedlings (data from Read & Hill 1985).

intercept less radiation, and produce less stemwood (Cannell & Grace 1993, Nambiar & Sands 1993). The amount of available light depends on the filtering properties of the canopy above, already capturing this resource, and the architecture of the shaded plant (Rossignol et al. 1998). Taller plants strongly inhibit the growth and subsequent survival or lower plants by interplant asymmetric competition, simply because they consume light energy and therefore reduce the availability for other plants (Goldberg 1997, Tilman 1997). The fact that all trees, regardless of species, give priority to height growth over diameter growth (King 1990, Oliver & Larson 1996, Kozlowsky & Pallardy 1997a), is demonstrated by the different behaviour of both variables, and by the independence between age and height growth for *Nothofagus dombeyi*.

In silviculture, many practical problems require understanding of the performance of trees with different temperaments in the same forest. For instance, under a regime of logging a stepwise change in the light environment and soil condition occurs in the stand, leading to a dramatic and immediate impact on remaining trees, saplings, and seedlings. Some species profit by this change, others do not or are harmed, and the future composition and structure hence will not be the same as the preceding one. The standard technique of "high thinning" (thinning of large trees) to manage wood production is an appropriate practise to reallocate growing space to different trees mostly when competition is primarily one–sided. Removing large trees will artificially shift growing opportunities to lower trees, whereas "low thinning" (removing small or weak trees) will have little effect on the overall growth of the stand (Smith et al. 1997). Rational forest management based of the Patagonian association studied here must take into account the differential effects found in the present study, in relation to the spatial and temporal scales of diameter and height growth in each tree species.

Growth and dioecy

Reproductive males and females of *Austrocedrus chilensis* that compose the stand under study grow in diameter and height at statistically similar rates. To address the apparent conflict between this result, and those previously reported that agree with the allocation theory in relation to sex for *Austrocedrus chilensis*, the following hypotheses can be proposed: a) although females invest more than males, there is no a negative correlation between vegetative growth and reproductive investment, b) there is a trade–off between reproductive and vegetative function, nevertheless i) the trade–off involves another element apart from carbohydrates (e.g., nutrient), or another plant structure apart from timber volume (e.g., root and/or leaf biomass), ii) volume growth and reproduction are not directly and mutually compensating functions: plant structures contributes to more thát only one function (Oldeman 1990), iii) sex–specific allocation phenology, linked to tree architecture (Rossignol et al. 1998), masks an underlying trade–off: a female strategy may comprise a larger investment in carbon–processing organs at the onset of the flowering period, when its investment in reproductive structures is frequently less in comparison with males, iv) the trade–off is also camouflaged because the sex class that invests more in reproduction shows a higher rate of primary productivity, v) under particular conditions plants are incapable to express the reproduction capacity, therefore its negative incidence on vegetative growth is negligible. Although for *Austrocedrus chilensis* there is no quantitative measurement of allocation to reproductive structures, repeated field observations are compatible with the last proposition: within the examined site, trees allocate low amounts of resources to reproduction regardless of sex class.

In *Austrocedrus chilensis* forests, the standing biomass of a particular site and the individual abundance of reproductive organs are inversely proportional: isolated trees exhibit notably developed and expanded crowns with many cones, while trees in crowded stands show small crowns with few cones. In pure woodlands (PW), pure forests (PF), and mixed forests with *Nothofagus dombeyi* (MF), *Austrocedrus chilensis* density is estimated in 268, 798, and 460 adults ha^{-1}, respectively (Dezzotti & Sancholuz 1991). During a 6-year study period, in these three forest types, seed production in *Austrocedrus chilensis* was estimated to be $350*10^6$, $920*10^6$, and $180*10^6$ seeds $ha^{-1}yr^{-1}$, respectively, values that differ statistically (Lucero 1996, Sancholuz et al. unpubl.). Combining both variables, an individual production of $1.31*10^6$, $1.15*10^6$, and $0.39*10^6$ seeds yr^{-1} is calculated for the three forest types, respectively. These values are inversely proportional to the stand volume for the three associations, estimated to be 57.3, 286.9, 570.8 m^3ha^{-1}, respectively (Dezzotti & Sancholuz 1991). In mixed forests, *Austrocedrus chilensis* trees exhibit a seed production substantially lower than trees of this species in the other forest types. This is explained by a high tree density and biomass, and particularly the presence of large–sized, fast–growing *Nothofagus dombeyi* trees. Therefore, the major regulation factor is expected for light. If trees in structurally well–developed, dense forests are unable to express the same reproductive potential as isolated plants within open woodlands, the reproductive incidence on the budget of energy and nutrient should be marginal and differences in biomass growth between sexes would not be expected.

The direct effect of light intensity on tree reproduction has been demonstrated in many experimental studies in forests and orchards, involving different trees (e.g., Jackson & Palmer 1977, Wright & van Schaik 1994), and different fruit positions in individual crowns (e.g., Kappel & Flore 1983). Initiation of flower buds, fruit set, and number, size, weight, and quality of fruits and cones is reduced by shade cast both by neighbouring trees and by the surrounding organs of the crown itself. In woody perennial plants, the relative investment for reproductive structures in male and female function, calculated as a proportion of annual production, increases with plant size, as shown for different species over long–term studies (Piñero et al. 1982, Oyama & Dirzo 1988, Bazzaz & Ackerly 1992). These investments are highly regulated by tree architecture as a determinant of the sapstream (Oldeman 1990). A more comprehensive understanding of the effects of physical environment, vegetation structure, tree architecture, and reproductive growth in *Austrocedrus chilensis* is considered relevant in terms of the biological, ecological, and silvicultural implications. The hypotheses suggested here may serve as empirical research directions for future studies.

Stand development

This study brings elements of proof that the current *Austrocedrus chilensis*–dominated mixed forest depends on large–scale and heavy impacts and not on small and light ones. Without such massive events, it will advance towards a later phase of forest development dominated by *Nothofagus dombeyi*. Changes in the abiotic environment with an improvement of the humidity condition at local level, probably resulted from abundant recruitment of xeric *Austrocedrus chilensis* trees during stand initiation, about 130 years ago. After canopy closure, site improvement by the early tree occupants made the area more suitable for the abundant colonisation by mesic, faster growing *Nothofagus dombeyi* seedlings and saplings, which define the present–day understorey reinitiation stage of the forest. If the current trends continue, it is expected that a shift in dominance towards *Nothofagus dombeyi* will occur, unless new, heavy impacts reinitiates secondary succession leading probably again to an even–aged forest dominated by *Austrocedrus chilensis*.

During the last four decades of development, a comparatively more intense establishment of *Nothofagus dombeyi* was observed comprising 84% of the total density of seedlings. At the start of secondary succession, the stand was first colonised by *Austrocedrus chilensis*. Like many northern and southern hemisphere gymnosperms (Spies & Franklin 1989, Oldeman 1990, Kuiper 1994, Enright & Odgen 1995), *Austrocedrus chilensis* is a climax component in edaphically or climatically suboptimal locations whereas it is a successional plant in more favourable, mesic sites. However, the properties expected in early successional plants, such as rapid growth and high allocation of metabolites to early and vast reproduction (Grime 1979, Oldeman & van Dijk 1991, Bazzaz 1996, Crawley 1997a), are not present in *Austrocedrus chilensis*. It exhibits the syndromes frequently found in many southern conifers: a light–demanding temperament, a slow–growing strategy, and a long life–cycle. The site was later invaded by *Nothofagus dombeyi*. This is a light–demanding, rapid growing pioneer species. It regenerates episodically and massively in large gaps created by heavy, landscape–scale impacts during primary and secondary successions, comprising pure and mixed stands with broadleaved trees.

In the absence of huge impacts, changes in forest architecture over time account for interspecific differences in recruitment, growth rates, and mutual interaction, basically resulting in a local decline of the conifer component. However, the combination of a great longevity and a light–demanding temperament of *Austrocedrus chilensis*, as observed in other southern conifers (Read & Hill 1988), implies that frequent to very infrequent heavy impacts over large surfaces would be required to maintain their abundance in the landscape. These long–lived plants that benefit from extensive vegetation destruction expand their range when large areas are opened up for colonisation, and retract when crowded conditions with small impacts prevail over longer periods (Enright & Odgen 1995). In some cases, conifers tend to attain greater sizes given the longer growth period associated to their greater longevity. For instance, in old–growth stands *Agathis australis* reaches dominance by outliving the pioneer angiosperm species and by being larger than other canopy dominant angiosperms (Odgen & Stewart 1995). *Nothofagus dombeyi* attains larger sizes, given a more rapid growth rate over a more extended period. *Austrocedrus chilensis* is very sensible to one–sided competition. However, neither *Austrocedrus chilensis* nor *Nothofagus dombeyi* can overtop each other when adults.

These results and literature reveal that divergent development patterns occur in *Austrocedrus chilensis* and *Nothofagus dombeyi* forests. Veblen et al.(1980, 1981), examining stands at high and mid–elevations in Chile, conclude that periodic exogenous impacts prevent the successional replacement of *Nothofagus dombeyi* by the shade–tolerant tree species that develop underneath the canopy, in gaps caused by treefall during forest maturation. Armesto & Figueroa (1987) also suggested *Nothofagus dombeyi* as an early seral species in a Chilean forest at a lower altitude. In Argentina, Veblen & Lorenz (1987), and Veblen (1989) did not find evidence of mutual replacement in *Nothofagus dombeyi–Austrocedrus chilensis* mixed forests. The stands examined comprised even–aged populations recruited at the same time. There were no saplings beneath the canopy, and both tree species established themselves synchronously and abundantly in treefall gaps. In a mixed stand with the same composition, several characteristics were reported in an unpublished paper indicating a similar development sequence (Anonymous 1994). Both populations followed a normal age frequency distribution and a difference of about 35 years between the oldest individuals of *Austrocedrus chilensis* (range 35 to 115 years) and the oldest individuals of *Nothofagus dombeyi* (20 to 80 years) was found. The successful recruitment of *Nothofagus dombeyi* saplings in light–gaps in Argentinean forests, as compared with their failure observed in Chilean forests, is explained by the absence in Argentina of shade–tolerant shrub and tree species interacting with *Nothofagus dombeyi* (Veblen 1989). Previous studies proposed stability of *Austrocedrus chilensis-Nothofagus dombeyi* mixed forests in northern Patagonia. The present study does not confirm this, probably due to the presence of very different sites, eliciting divergent responses in differently adapted species. Extremes of these responses are reflected in the occurrence of pure *Austrocedrus chilensis* and *Nothofagus dombeyi* forests, in close proximity to each other. Indeed, no one and unique set of architecture and dynamics can prevail in the transition zone, where the ranges of both species overlap and mixed forests arise. As we found, there are different versions instead, depending on the position of the forest along the environmental gradient, and its effect on species performance. Conifer age discontinuity formerly was interpreted as an indication of species retreat. However, it should be interpreted from the non–equilibrium successional perspective originally proposed by Watt (1947), and generalised by Oldeman (1990) under the name of "ecuilibrium" (eco–unit equilibrium). A forest community is a kaleidoscopic mosaic of patches of different ages (eco–units), characterised by cyclic vegetational changes occurring at lower spatial scales explained by differential responses of species to perturbation. This abstraction was the basis of several models of forest development (Hallé et al. 1978, Bormann & Likens 1979, Oliver 1981, Peet & Christensen 1987, Oldeman 1990). Symmetric age structures are therefore local in extent.

In an early study, Kalela (1941) analysed the size structure of stands composed of large

Nothofagus dombeyi and small *Austrocedrus chilensis* trees. Erroneously assuming that the smaller trees were also younger and invading drought–tolerant trees, he interpreted the data as indicative of "successional replacement" of a mesic flora by a xeric flora, in response to a trend towards a climatically induced aridification in northern Patagonia. This idea had been proposed previously by Auer (1933), who suggested that changes in the boundary of the forest / steppe ecotone were occurring, with an expansion of the steppe westward and a consequent retreat of the forest. This was the tune of those times, with scientists like Aubréville in Africa and van Steenis in Indonesia paying attention to the moving borders between wet forests and dry savannas. Later, vegetational, palynological, and dendrochronological evidences failed to support the hypothesis of the natural aridification process in Patagonia (Thomasson 1959, Eriksen 1975, LaMarche et al. 1979, Markgraf 1983, 1987, Veblen & Lorenz 1988). The results presented here also falsify Auer's and Kalela's hypotheses and rather show the opposite, a trend from a xeric to a mesic flora.

Minimum area

For tree–dominated communities in temperate forests, Mueller–Dombois & Ellenberg (1974) claim that the minimum area varies between 200 and 500 m^2. Westhoff & van der Maarel (1978) and Knapp (1984) suggest that the minimum area for this vegetation type varies between 100 and 500m^2. Bormann (1953) determined a minimum area between 560 and 1,400m^2, analysing the basal area of a deciduous forests in eastern North America composed of arborescent *Quercus* and *Carya* (Juglandaceae) species. Lorimer (1985) found that an area in between 100 and 800m^2 is appropriate for the study of structurally simple stands, such as those composed of *Picea* and *Abies* species in the boreal coniferous forests that form extended even–aged stands. However, this author suggests a minimum area of some 5,000m^2 to characterise more complex communities, such as the mixed deciduous forests composed of *Tsuga*, *Betula*, and *Acer* species. Krebs (1989) found that a plot of around 360m^2 gives an acceptable measure of the density in an *Alnus*–dominated forests.

The results from the present study indicate that a sampling area up to 500m^2, as is generally suggested in literature (Bormann 1953, Mueller–Dombois & Ellenberg 1974, Westhoff & van der Maarel 1978, Oldeman 1983, 1990, Knapp 1984, Krebs 1989), is too small for the statistical analysis of the structure and growth of the forest composed of *Austrocedrus chilensis* and *Nothofagus dombeyi*. A sampling area of 1,000m^2 gives mean values of the structural variables equivalent to those measured using a larger area. However, the accuracy of the estimates for all the variables examined varies between 30% and 49%, which is rather poor. In exclusively statistical terms, an area of around 5,600m^2 should be surveyed in order to obtain relative errors for the estimates equal or lower than 20% of the mean. Lorimer (1985) advised the same size area for the ecological analysis of forests belonging to similar physiognomic types as the present. This corresponds amazingly well to van Rompaey's (1993) conclusion, based on Detrended Correspondance Analysis, that vegetation limits on West African maps of forest types were due for 21% to the methods used by the scientists.

Knowledge on the statistical advantage obtained by plot size enlargement is important during the final election of the appropriate sampling design. However, even within half a hectare one must consider the fact established by van Rompaey (1993) in his forest gradients analysis, that no really homogeneous sites of this size exist, and hence statistical replication is inherently impossible in forests. His method of contour sampling of large forest trees addressed another fundamental problem. For plants of such widely divergent sizes such as *Nothofagus dombeyi*, intermediate *Chusquea* species, or tiny mosses, minimal areas inherently lies at different scales. The implications of these inherent properties, heterogeneity, and nested scales have been considered by Rossignol et al.(1998). One of the major challenges in vegetation science is to find ways and means to account for the apparently inherent, high margins of error. They are certainly linked to matters of scale, to the fuzzy character of natural vegetation limits, and to the fact that natural areas are not squares, circles or pixels.

The present study summarised the evolutionary and life cycle characteristics of the main tree species of the Patagonian association concerned. It presented a new perspective on its dynamics fitting them in a comprehensible and conceptual model of vegetation development, as an expression of adaptive responses, opportunistic adjustments, and biotic interactions. However, were are still distant from a profound comprehension of these fascinating ecosystems and captivating trees. The complete knowledge should address the remaining and profound problems of complexity and diversity, which can not be understood by applying only simple mathematical and statitical methods.

References

Aceituno P, H Fuenzalida & B Rosenblüth. 1993. Climate along the extratropical west coast of South America. In: Earth system responses to global change: contrasts between North and South America. HA Mooney, ER Fuentes & BI Kronberg (eds.). Chapter 4:61–69. Academic Press. San Diego.

Adams WT, SH Strauss, DL Copes & AR Griffin (eds.). 1992. Population genetics of woody trees. Kluwer. Dordretch.

Agren J. 1988. Sexual differences in biomass and nutrient allocation in the dioecious *Rubus chamaemorus*. Ecology 69:962–973.

Aguilera L & A Fehlandt. 1981. Desarrollo inicial de *Nothofagus alpina* (Poepp. et Endl.) Oerst., *Nothofagus obliqua* (Mirb.) Bl., y *Nothofagus dombeyi* (Mirb.) Bl. bajo tres grados de sombra. Tesis de grado. Facultad de Ingeniería Forestal. Universidad Austral de Chile. Valdivia.

Alaback PB. 1991. Comparison of temperate rainforests of the Americas. Revista Chilena de Historia Natural 64:399–412.

Alban DH, DA Peralta & BE Schlaegel. 1978. Biomass and nutrient distribution in aspen, pine, and spruce stands on the same soil type in Minnesota. Canadian Journal of Forest Research 8:290–299.

Alberdi M. 1995. Ecofisiología de especies leñosas de los bosques higrófilos templados de Chile: resistencia a la sequía y bajas temperaturas. In: Ecología de los bosques nativos de Chile. JJ Armesto, C Villagrán & MK Arroyo (eds.). Chapter 15:279–300. Universitaria. Santiago de Chile.

Alfonso J. 1940. Los Bosques Subantárticos. Ingeniería Agronómica 2(10):35–46. Buenos Aires.

Allen RB & KH Platt. 1990. Annual seedfall variation in *Nothofagus solandri* (Fagaceae), Canterbury, New Zealand. Oikos 57:199–206.

Allen G & J Antos. 1993. Sex ratio variation in the dioecious shrub *Oemleria cerasiformis*. The American Naturalist 141(4): 537–553.

Almeyda AE & SF Sáez. 1958. Recopilación de datos climáticos de Chile y mapas sinópticos respectivos. Ministerio de Agricultura. Santiago de Chile.

Amthor JS, DS Gill & FH Bormann. 1990. Autumnal leaf conductance and apparent photosynthesis by saplings and sprouts in a recently disturbed northern hardwood forest. Oecologia 84:93–95.

Anonymous. 1994. Estructura y dinámica de un boque templado de *Austrocedrus chilensis* y *Nothofagus dombeyi* en el noroeste de la Patagonia argentina. Trabajo de campo. Curso de Ecología Forestal. Universidad Nacional del Comahue. S.C.de Bariloche. Unpublished.

Anziano AF. 1962. Acción de los animales sobre la flora. Anales de Parques Nacionales 9:107–112.

APN. 1986. Plan general de manejo del Parque Nacional Nahuel Huapi. Administración de Parques Nacionales / Consejo Federal de Inversiones. Buenos Aires.

Archivald E. 1949. The specific character of plant communities. Journal of Ecology 37:260–274.

Archivold OW. 1995. Ecology of world vegetation. Chapman & Hall. London.

Armesto JJ, J Mitchell & C Villagrán. 1986. A comparison of spatial patterns of trees in some tropical and temperate forests. Biotropica 18(1):1–11.

Armesto JJ & J Figueroa. 1987. Stand structure and dynamics in the temperate rain forests of Chiloé Archipiélago, Chile. Journal of Biogeography 14:367–376.

Armesto JJ & ER Fuentes. 1988. Tree species regeneration in a mid-elevation, temperate rain forest in Isla de Chiloé, Chile. Vegetatio 74:151–159.

Armesto JJ, I Casassa & O Dollenz. 1992. Age structure and dynamics of Patagonean beech forests in Torres del Paine National Park, Chile. Vegetatio 98:13–22.

Armesto JJ, P León–Lobos & MK Arroyo. 1995. Los bosques templados de Chile y Argentina: una isla biogeográfica. In: Ecología de los bosques nativos de Chile. JJ Armesto, C Villagrán & MK Arroyo (eds.). Chapter 1:23–28. Universitaria. Santiago de Chile.

Arroyo MTK, JJ Armesto, F Squeo & J Gutiérrez. 1993. Global change: flora and vegetation of Chile. In: Earth system responses to global change: contrasts between North and South America. HA Mooney, ER Fuentes & BI Kronberg (eds.). Chapter 17:239–263. Academic Press. San Diego.

Arroyo MTK, M Riveros, A Peñaloza, L Cavieres & AM Faggi. 1996. Phytogeographic relationships and regional richness patterns of the cool temperate rainforest flora of Southern South America. In: High latitude rain forests and associated ecosystems of the west coast of America. RG Lawford, PB Alaback & ER Fuentes (eds.).

Chapter 8:134–172. Springer–Verlag. New York.

Ashton P. 1965. Some problems arising in the sampling of mixed rain forest communities for floristic studies. Symposium of ecological research in humid tropics vegetation. Pag.235–240. Tokyo Press. Tokyo.

Ashworth AC, V Markgraf & C Villagrán. 1991. Late Quaternary climatic history of the Chilean Channels based on fossil pollen and beetle analysis, with an analysis of the modern vegetation and pollen rain. Journal of Quaternary Science 6(4):279–291.

Attiwill PM. 1994. The impact of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63:247–300.

Auer V.1933. Verschiebungen der Wald– und Steppengebiete Feuerlands in post–glazialer. Zeitung Acta Geographica 5:1–313.

Barkman J. 1989. A critical evaluation of minimum area concepts. Vegetatio 85:89–104.

Barnes B, D Zak, S Denton & S Spurr. 1998. Forest ecology. John Wiley & Sons. New York.

Barros V, V Cordon, C Moyano, R Méndez, J Forquera & O Pizzio. 1983. Cartas de precipitación de la zona oeste de las provincias de Río Negro y Neuquén. Universidad Nacional del Comahue / Centro Nacional Patagónico. Cinco Saltos.

Bava J & J Puig. 1992. Regeneración natural de lenga. Publicación técnica 8. Centro de Investigación y Extensión Forestal Andino Patagónico (CIEFAP). Esquel.

Bawa KS. 1980. Evolution of dioecy in flowering plants. Annual Review of Ecology and Systematics 11:15–39.

Bazzaz FA. 1983. Characteristics of populations in relation to impact in natural and man–modified ecosystems. In: Impact and ecosystems: components of response. HA Mooney & M Godron (eds.). Ecological Studies 44:259–275. Springer–Verlag. Berlin.

Bazzaz FA. 1996. Plants in changing environments. Cambridge University Press. Cambridge.

Bazzaz FA & DD Ackerly. 1992. Reproductive allocation and reproductive effort in plants. In: Seeds: the ecology of regeneration in plant communities. M Fenner (ed.). CAB International. Oxon.

Beard JS. 1990. Temperate forests of the southern hemisphere. Vegetatio 89:7–10.

Benoit I. 1989. Libro rojo de la flora terrestre de Chile. Corporación Forestal Nacional. Ministerio de Agricultura. Santiago de Chile.

Biswas C & BM Johri. 1997. The gymnosperms. Narosa Publishing House. New Dehli.

Bond WJ. 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm pesistence. Biological Journal of the Linnean Society 36:227–249.

Boninsegna J & R Holmes. 1978. Breve descripción de un relicto de *Austrocedrus chilensis* (D.Don) Endl. en Huinganco (Pcia. del Neuquén). Anales IANIGLA / CONICET 1977(4):115–123.

Bormann FH. 1953. The statistical efficiency of sample plot size and shape in forest ecology. Ecology 34(3):474–487.

Bormann FH. 1965. Changes in the growth pattern of white pine trees undergoing supression. Ecology 46:269–277.

Bormann FH & G Likens. 1979. Pattern and process in a forested ecosystem. Springer–Verlag. New York.

Brión C, D Grigera, J Puntieri & E Rapoport. 1987. Plantas exóticas en bosques de *Nothofagus*. Comparaciones preliminares entre el norte de la Patagonia y Tierra del Fuego. Monografías Academia Nacional de Ciencias Exactas, Físicas y Naturales 4:37–47. Buenos Aires.

Brión C, D Grigera & P Rosso. 1993. The reproduction of *Austrocedrus chilensis* (D.Don) Florin et Boutelje. Comptes Rendus. Academie des Science Paris 316:721–724.

Bruno J. 1982. Los incendios forestales en los Parques Nacionales. Estudio estadístico y análisis de su incidencia. Internal Report Administración de Parques Nacionales. Buenos Aires.

Bryant D, D Nielsen & L Tangley. 1997. The last frontier forests: ecosystems and economies on the edge. World Resources Institute. Washington.

Bullock SH & KS Bawa. 1981. Sexual dimorphism and the annual flowering pattern in *Jacaratia dolichaula* (D.Smith) Woodson (Caricaceae) in a Costa Rican forest. Ecology 62:1494–1504.

Burger WC. 1981. Heresy revised: the monocot theory of angiosperm origin. Evolutionary Theory 5:189–225.

Burschel P, C Gallegos, O Martínez & W Moll. 1976. Composición y dinámica regenerativa de un bosque virgen mixto de raulí y coigüe. Bosque 1(2):55–74.

Bustamante R. 1995. Depredación de semillas en bosques templados de Chile. In: Ecología de los bosques nativos de Chile. JJ Armesto, C Villagrán & MK Arroyo (eds.). Chapter 14:265–278. Universitaria. Santiago de Chile.

Cabrera LA. 1976. Regiones fitogeográficas de la

República Argentina. ACME. Buenos Aires.

Cain S. 1938. The species–area curve. The American Midland Naturalist 19:573–581.

Caldwell JM, EI Sucoff & RK Dixon. 1995. Grass interference limits resource availability and reduces growth of juvenile red pine in the field. New Forests 10:1–15.

Cannell MGR, P Rothery & ED Ford. 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. Annals of Botany 53:349–362.

Cannell MGR & J Grace. 1993. Competition for light: detection, measurement, and quantification. Canadian Journal of Forest Research 23:1969–1979.

Cao K, R Peters & RAA Oldeman. 1995. Climatic range and distribution of Chinese *Fagus* species. Journal of Vegetation Science 6:317–324.

Cassie VD. 1954. New Zealand conifers. Journal of the Arnold Arboretum 35:268–273.

Chamov EL & J Bull. 1977. When is sex environmentally determined? Nature 266:828–830.

CIEFAP. 1993. Dinámica del ataque de liebre europea en plantaciones de pinos. Centro de Investigación y Extensión Forestal de los Boques Andino–Patagónicos (CIEFAP). Esquel.

Clapperton C. 1990. Quaternary glaciations in the southern hemisphere: an overview. Quaternary Science Review 9:299–304.

Clapperton C. 1993. Quaternary geology and geomorphology of South America. Elsevier. Amsterdam.

Cliff A & J Ord. 1981. Spatial processes: models and applications. Pion. London.

Cody ML. 1966. A general theory of clutch size. Evolution 20:174–184.

Coetzee JA. 1993. African flora since the terminal Jurassic. In: Biological relationships between Africa and South America. Proceedings 37th Annual Systematic Symposium. P Goldblatt (ed.). Chapter 3:37–61.

Connell JH, J Tracey & L Webb. 1984. Compensatory recruitment, growth and mortality as a factors maintaining rain forest tree diversity. Ecological Monographs 54:141–164.

Cordon V, J Forquera & J Gastiazoro. 1993. Estudio microclimático del área cordillerana del sudoeste de la provincia de Río Negro. Universidad Nacional del Comahue. Cinco Saltos.

Correa MN. 1969–1985. Flora patagónica. Five volumes. Colección Científica. Instituto Nacional de Tecnología Agropecuaria. Buenos Aires.

Correa Luna H & M Dimitri. 1969. Las comunidades florísticas de la cuenca del río Manso Superior. Dirección General de Parques Nacionales / Fundación Bariloche. Buenos Aires.

Costantino I. 1958. Primeros resultados de las parcelas permanentes de *Libocedrus chilensis*. Revista de la Facultad de Agronomía (La Plata) 34(2):131–159.

Cottam G & JT Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Crawley MJ. 1997a. Life history and environment. In: Plant ecology. MJ Crawley (ed.). Chapter 4:73–131. Blackwell. Oxford.

Crawley MJ. 1997b. Sex. In: Plant ecology. MJ Crawley (ed.). Chapter 6:156–213. Blackwell. Oxford.

Crawley MJ. 1997c. The structure of plant communities. In: Plant ecology. MJ Crawley (ed.). Chapter 14:475–531. Blackwell. Oxford.

Cronquist A.1988. The evolution and classification of flowering plants. 2nd edition. The New York Botanical Garden. New York.

Crane PR. 1995. History of a green kingdom. Kew (Spring):18–25.

Cruden RW & DL Lyon. 1985. Patterns of biomass allocation to male and female functions in plants with different mating systems. Oecologia 66:299–306.

Daciuk J. 1973. Notas faunísticas y bioecológicas de Península Valdéz y Patagonia. VII. Estudio de la coacción del ganado en la cuenca del río Manso Superior. Physis 32(85):383–402.

Dahl E. 1960. Some measures of uniformity in vegetational analysis. Ecology 41:805–808.

Dalziel IW. 1992. Antarctica: a tale of two supercontinents? Annual Review of Earth and Planetary Sciences 20:501–526.

Darwin C. 1839. Journal of researches into the geology and natural history of the various countries visited by H.M.S.Beagle, under the command of Captain Fitzroy, R.N. from 1832 to 1836. John Murray. London.

Dawson T & L Bliss. 1989. Pattern of water use and the tissue water relations in the dioecious shrub, *Salix arctica*: the physiological basis for habitat partitioning between the sexes. Oecologia 79:332–343.

De Fina A. 1972. El clima de la región de los Bosques Andino–Patagónicos argentinos. In: La región de los Bosques Andino–Patagónicos. M Dimitri (ed.). Tomo 10: 35–58. Instituto Nacional de Tecnología Agropecuaria. Buenos Aires.

Delph LF, Y Lu & LD Jayne. 1993. Patterns of resource allocation in a dioecious *Carex* (Cyperaceae). American Jornal of Botany 80: 607–615.

Delph LF & TR Meagher. 1995. Sexual dimorphism masks life history trade–offs in the dioecious plant *Silene latifolia*. Ecology 76(3):775–785.

Dettmann ME, DT Pocknall, EJ Romero & MC Zamaloa. 1990. *Nothofagidites* Erdtman ex Potonie 1960; a catalogue of species with notes on the paleogeographic distribution of *Nothofagus* Bl. (southern beech). New Zealand Geological Survey Palaeontological Bulletin 60:1–79.

Dezzotti A. 1995. Autocorrelación espacial de la edad de *Austrocedrus chilensis*. Proceedings 17th Reunión Argentina de Ecología. Mar del Plata.

Dezzotti A. 1996a. *Austrocedrus chilensis* and *Nothofagus dombeyi* stand development during secondary succession in the temperate forest of NW Patagonia, Argentina. Forest Ecology and Management 89:125–137.

Dezzotti A. 1996b. Area mínima de un bosque templado basada en la abundancia, el tamaño y el crecimiento de las especies dominantes. Medio Ambiente 13(1):64–74.

Dezzotti A. 1999. Efecto de la competencia sobre el crecimiento de un bosque templado mixto. Proceedings 19th Congreso de la Sociedad Argentina de Ecología. S.M.de Tucumán.

Dezzotti A & L Sancholuz. 1991. Los bosques de *Austrocedrus chilensis* en Argentina: ubicación, estructura y crecimiento. Bosque 12(2):43–52.

Dezzotti A & RAA.Oldeman. 1994. Crecimiento de un bosque mixto en el noroeste de la Patagonia: diferencias entre las especies y sus estados de desarrollo. Proceedings 6th Congreso Latinoamericano de Botánica. Mar del Plata.

Dezzotti A & L Sancholuz. 1995. ¿Existe crecimiento diferencial dependiente del sexo en *Austrocedrus chilensis*? Proceedings 4th Jornadas Forestales Patagónicas:151–159. San Martín de los Andes.

Dietvorst P, E van der Maarel & H van der Putten. 1982. A new approach to the minimum area of plant communities. Vegetatio 50:77–93.

Dimitri M. 1972. La región de los bosques Andino–Patagónicos. Sinopsis general. Colección Científica. Tomo 10. Instituto Nacional de Tecnología Agropecuaria. Buenos Aires.

Donoso C. 1984. Hibridación natural entre *Nothofagus betuloides* Mirb.(Oerst) y *N.nitida* (Phil.) Krasser. Medio Ambiente 7:9–16.

Donoso C. 1993. Bosques templados de Chile y Argentina: variación, estructura y dinámica. Universitaria. Santiago de Chile.

Donoso C & A Cabello. 1978. Antecedentes fenológicos y de germinación de especies leñosas chilenas. Ciencias Forestales: 31–41.

Donoso C & L Landrum. 1979. *Nothofagus leonii* Espinosa, a natural hybrid between *N.obliqua* (Mirb.) Oerst. and *N.glauca* (Phil.) Krasser. New Zealand Journal of Botany 17:353–360.

Donoso C & J Atienza. 1983. Hibridación natural entre especies de *Nothofagus* siempreverdes en Chile. Bosque 5:21–34.

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

Donoso C, R Grez, B Escobar & P Real. 1984. Estructura y dinámica de bosques del tipo forestal siempreverde en un sector de Chiloé insular. Bosque 5:82–104.

Donoso C, B Escobar & J Urrutia. 1985. Estructura y estrategias regenerativas de un bosque virgen de ulmo (*Eucryphia cordifolia* Dav.) y tepa (*Laurelia philippiana* Phil.) Looser en Chiloé, Chile. Revista Chilena de Historia Natural 58:171–186.

Donoso C, M Cortés & B Escobar. 1986. Germinación de semillas y técnicas de vivero y plantaciones para especies de los tipos forestales de la X Región. Informe 102. CONAF – Universidad Austral de Chile. Valdivia.

Donoso C, J Morales & M Romero. 1990. Hibridación natural entre roble (*Nothofagus obliqua* (Mirb.) Oerst.) y raulí (*Nothofagus alpina* (Poepp.& Endl.) Oerst.), en bosques del sur de Chile. Revista Chilena de Historia Natural 63:49–60.

Donoso C, M Hernández & C Navarro. 1993. Valores de producción de semillas y hojarasca de diferentes especies del tipo forestal siempreverde de la Cordillera de la Costa de Valdivia obtenidos durante un período de 10 años. Bosque 14(2):65–84.

Donoso C & A Lara. 1995. Utilización de los bosques nativos de Chile: pasado, presente y futuro. In: Ecología de los bosques nativos de Chile. JJ Armesto, C Villagrán & MK Arroyo (eds.). Chapter 19:363–387. Universitaria. Santiago de Chile.

Dony J. 1977. The expectation of plant records from prescribed areas. Watsonia 5:377–385.

Doyle JA & MJ Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. The Botanical Review 52:321–431.

Duncan R & G Stewart. 1991. The temporal and spatial analysis of tree age distributions. Canadian Journal of Forest Research 21:1703–1710.

Eckenwalder JE. 1976. Re-evaluation of Cupressaceae and Taxodiaceae: a proposed merger. Madroño 23(5):237–300.

Edelin C. 1977. Images de l'architecture des Conifères. PhD thesis. Academie de Montpellier. Université de Sciences et Techniques du Langedoc. Montpellier.

Elmqvist T, R Gates, K Harper & H Gardfjell. 1991. Flowering in males and females of a Utah willow, *Salix rigida*, and effects on growth, tannins, phenolic glycosides and sugars. Oikos 61:65–72.

Enright NJ, RS Hill & TT Veblen. 1995. The southern conifers: an introduction. In: The ecology of southern conifers. NJ Enright & RS Hill (eds.). Chapter 1: 1–9. Melbourne University Press. Carlton.

Enright NJ & J Odgen. 1995. The southern conifers: a synthesis. In: The ecology of southern conifers. NJ Enright & RS Hill (eds.). Chapter 12: 271–287. Melbourne University Press. Carlton.

Eriksen W. 1970. Kolonization und tourismus in Ostpatagonien. Bonnes Geographische Abhandlunger 43:290.

Eriksen W. 1975. Disruptions in the ecosystems of the steppe and forest regions of Patagonia by climate and man. Applied Science and Development 6:127–142.

Eskuche U. 1973. Estudios fitosociológicos en el norte de Patagonia. Phytocoenologia 1(1):64–113.

Espinoza M. 1972. Alcances sobre las condiciones de luz como factor importante en la regeneración natural del bosque tipo raulí (*Nothofagus alpina* Poepp. et Endl., Kasser) y coigüe (*Nothofagus dombeyi* (Mirb.) Oerst.). Tesis de grado. Facultad de Ingeniería Forestal. Universidad Austral de Chile. Valdivia.

FAO. 1990. FAO–UNESCO soil map of the world. Revised legend. Soils Bulletin 60. Food and Agriculture Organization. Rome.

Florin R. 1963. The distribution of conifer and taxod genera in time and space. Acta Horti Bergiani 20(4):121–312.

Florin R & JB Boutelje. 1954. External morphology and epidermal structure of leaves in the genus *Libocedrus*, s.lat. Acta Horti Bergiani 17(2):1–37.

Font Quer P. 1974. Botánica pintoresca. Ramón Sopena. Barcelona.

Frangi J. 1976. Descripción florístico–estructural de un stand de bosque de *Nothofagus dombeyi* en lago Gutiérrez (Provincia de Río Negro). Darwiniana 20:577–585.

Franklin J. 1988. Pacific northwest forest. In: North American terrestrial vegetation. MG Barbour & WD Billings (eds.). p.103–130. Cambridge University Press. Cambridge.

Freeman DC, LG Klikoff & KT Harper. 1976. Differential resource utilization by the sexes of dioecious plants. Science 193:597–599.

Gadek PA & CJ Quinn. 1993. An analysis of relationships within the Cupressaceae sensu stricto based on rbcL sequences. Annals of the Missouri Botanical Garden 80:581–586.

Gamundi IJ. 1971. Las Cyttariales sudamericanas. Darwiniana 16:461–511.

Gaussen H. 1954. Expression des milieux par des formules écologiques: leur représentation cartographique. In: Les divisions écologiques du globe. Colloques Internationaux du CNRS:13–25. Paris.

Gibson N, PCJ Barker, PJ Cullen & A Shapcott. 1995. Conifers of southern Australia. In: The ecology of southern conifers. NJ Enright & RS Hill (eds.). Chapter 10: 223–251. Melbourne University Press. Carlton.

Givnish TJ. 1980. Ecological constraints on the evolution of breeding systems in seeds plants: dioecy and dispersal in gymnosperms. Evolution 34(5):959–972.

Glavac V, C Grillenberg, W Hakes & H Ziezold. 1992. On the nature of vegetation boundaries, undisturbed flood plain forest communities as an example: a contribution to the continuum / discontinuum controversy. Vegetatio 101:123–144.

Gobbi M. 1994. Regeneración de la vegetación en incendios recientes de bosques de "ciprés de la cordillera" (*Austrocedrus chilensis*) en el área del Parque Nacional Nahuel Huapi. Medio Ambiente 12(1):9–15.

Godley EJ. 1976. Sex ratio in *Clematis gentianoides* DC. New Zealand Journal of Botany 2:205–212.

Goldberg DE. 1997. Competitive ability: definitions, contingency and correlated traits. In: Plant life histories: ecology, phylogeny and evolution. JW Silvertown, M Franco & J Harper (eds.). Chapter 15:283–301. Cambridge University Press. Cambridge.

Goldblatt P. 1993. Biological relationships between Africa and South America: an overview. In: Biological relationships between Africa and South America. P Goldblatt (ed.). Proceedings 37th Annual Systematic Symposium. Chapter 1:3–14.

Yale University Press. New Haven.

Gómez I & GC Gallopín. 1982. Estudio ecológico integrado de la cuenca del río Manso Superior (Río Negro, Argentina). III. Las formas biológicas de las especies vasculares. Ecología Argentina 7:117–126.

Good B & S Whipple. 1982. Tree spatial patterns: South Carolina bottomland and swamp forests. Bulletin of the Torrey Botanical Club 109(4):529–536.

Goodall D. 1961. Objective methods for the classification of vegetation. IV. Pattern and minimal area. Australian Journal of Botany 9:162–196.

Goodall D. 1974. A new method for the analysis of spatial pattern by random pairing of quadrats. Vegetatio 29:135–146.

Goodall RN. 1979. Tierra del Fuego. Shanamaiim. Buenos Aires.

Gower ST, PB Reich & Y Son. 1993. Canopy dynamics and aboveground production of five tree species with different leaf longevities. Tree Physiology 12:327–345.

Greig–Smith P. 1952. The use of random and contiguous quadrats in the study of plant communities. Annals of Botany 16:293–316.

Greig–Smith P. 1983. Quantitative plant ecology. 3rd edition. Blackwell. Oxford.

Grimaldi D. 1999. The co–radiation of pollinating insects and angiosperms in the Cretaceous. Annals of the Missouri Botanical Garden 86(2):373–406.

Grime JP. 1979. Plant strategies and vegetation processes. John Wiley & Sons. Chichester.

Grime JP & R Hunt. 1975. Relative growth rate: its range and adaptive significance in a local flora. Journal of Ecology 63:393–422.

Grosse H. 1988a. Crecimiento de plantaciones de raulí y roble bajo dosel en dependencia del grado de luminosidad y fertilización. Ciencia e Investigación Forestal 2(5):13–30.

Grosse H. 1988b. Desarrollo de plantas de los géneros *Fagus* y *Nothofagus* en función de la luminosidad: revisión bibliográfica. Ciencia e Investigación Forestal 3(2):114–120.

Grosse H & M Bourke. 1988. Desarrollo de raulí en vivero bajo distintos niveles de luminosidad y espaciamiento. Ciencia e Investigación Forestal 3(2):1–11.

Grubb PJ. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Review 52:107–145.

Guerra P. 1986. Reconocimiento de especies del género *Nothofagus* en estado de plántulas. Publicación Asociación Amigos del Arbol. Tucumán.

Gunckel LH. 1948. La floración de la quila y del colihue en la Araucania. Ciencia e Investigación 4:91–95.

Gutiérrez E, VR Vallejo, J Romañá & J Fons. 1991. The subantarctic *Nothofagus* forests of Tierra del Fuego: distribution, structure and production. Oecologia Aquatica 10:351–366.

Haig D & M Westoby. 1991. Seed size, pollination costs and angiosperm success. Ecology and Evolution 5:231–247.

Hallé F, RAA Oldeman & P Tomlinson. 1978. Tropical trees and forests: an architectural analysis. Springer–Verlag. New York.

Harper J. 1977. Population biology of plants. Academic Press. New York.

Hart JA. 1987. A cladistic analysis of conifers: preliminary results. Journal of the Arnold Arboretum 68(3):269–307.

Heusser CJ. 1981. Palynology of the last interglacial – glacial cycle in midlatitudes of southern Chile. Quaternary Research 16:293–321.

Heusser CJ. 1984. Late Quaternary climates of Chile. In: Late paleoclimates of the southern hemisphere. JC Vogel (ed.). p.59–83. Balkema. Rotterdam.

Heusser CJ. 1989. Late Quaternary vegetation and climate of the southern Tierra del Fuego. Quternary Research 31:396–406.

Hevia F, ML Minoletti, KLM Decker & REJ Boerner. 1999. Foliar nitrogen and phosphorus dynamics of three Chilean *Nothofagus* (Fagaceae) species in relation to leaf lifespan. American Journal of Botany 86(3):447–455.

Hickey LJ & JA Doyle. 1977. Early Cretaceous fossil evidence for angiosperm evolution. The Botanical Review 43:3–104.

Hill RS. 1992. *Nothofagus*: evolution from a southern perspective. Trends in Ecology and Evolution 7(6):190–194.

Hill RS. 1995. Conifer origin, evolution and diversification in the southern hemisphere. In: The ecology of southern conifers. Enright NJ & RS Hill (eds.). Chapter 2: 10–29. Melbourne University Press. Carlton.

Hill RS & J Read. 1991. A revised infrageneric classification of *Nothofagus* (Fagaceae). Botanical Journal of the Linnean Society 105:37–72.

Hill RS & G Jordan. 1993. The evolutionary history of *Nothofagus* (Nothofagaceae). Australian Systematic of Botany 6:11–126.

Hill RS & ME Dettmann. 1996. Origin and diversification of the genus *Nothofagus*. In: The ecology and biogeography of *Nothofagus* forests. TT Veblen, RS Hill & J Read (eds.). Chapter 2:11–24. Yale University Press. New Haven.

Hochberg ME & JH Lawton. 1990. Competition between kingdoms. Trends in Ecology and Evolution 5(11):367–370.

Hoffmann A. 1982. Flora silvestre de Chile, zona austral. Fundación Claudio Gay. Santiago de Chile.

Holdgate MW. 1961. Vegetation and soils in the south Chilean islands. Journal of Ecology 49:559–580.

Hollin JT & DH Schilling. 1981. Late Wisconsin – Weichselian mountain glaciers and small ice caps. In: The last great ice sheets. G Denton & TJ Hughes (eds.). John Wiley & Sons. New York.

Holloway JT. 1954. Forests and climate in the South Island of New Zealand. Transactions of the Royal Society of New Zealand 82:329–410.

Hopkins B. 1955. The species–area relations of plant communities. Journal of Ecology 43:409–426.

Hueck K. 1978. Los bosques de Sudamérica: ecología, composición e importancia económica. Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ). Echbom.

Hughes NF. 1977. Palaeo–succession of earliest angiosperm evolution. The Botanical Review 43:105–127.

Humphries CJ, JM Cox & ES Nielsen. 1986. *Nothofagus* and its parasites: a cladistic approach to coevolution. In: Coevolution and systematics. AR Stone & DL Hawksworth (eds.). The Sistematics Association 32:55–76. Clarendon. Oxford.

Hutchings MJ. 1997. The structure of plants populations. In: Plant ecology. MJ Crawley (ed.). Chapter 11:325–358. Blackwell. Oxford.

Hyam R & R Pankhurst. 1995. Plants and their names: a concise dictionary. Oxford University Press. Oxford.

Innes JL. 1992. Structure of evergreen temperate rain forests on the Taitao Peninsula, southern Chile. Journal of Biogeography 19:555–562.

INTA. 1991. 23rd Congreso Argentino de la Ciencia del Suelo. S.C.Bariloche, 8–12/4/1991. Guía de campo. Instituto Nacional de Tecnología Agropecuaria. San Carlos de .Bariloche.

IUFRO. 1986. The standarization of simbols in forest mensuration. Proceedings Forest dynamics research in western and central Europe. J Fanta (ed.). Workshop of the International Union of Forestry Research Organisations. Appendix 2:281–316. Pudoc. Wageningen.

Jackson JE & JW Palmer. 1977. Effects of shade on the growth and cropping of apple trees. II. Experimental details and effects on vegetative growth. Journal of Horticultural Science 52: 245–252.

Jarvis PG & MS Jarvis. 1964. Growth rates in woody plants. Physiologia Plantarum 17:654–666.

Jarvis PG & JW Leverenz. 1983. Productivity of temperate, deciduous and evergreen forests. In: Encyclopedia of Plant Physiology New Series Volume 12D. Physiological Plant Ecology 4. OL Lange, PS Nobel, CB Osmond & H Ziegler (eds.). Chapter 8: 233–280. Springer–Verlag. Berlin.

Jones JH. 1986. Evolution of the Fagaceae: the implications of foliar features. Annals of the Missouri Botanical Garden 73:228–275.

Kalela E. 1941. Über die Holzarten und die durch die Klimatischen Verhältnisse verursachten Holzartenwechsel in den Wäldern Ostpatagoniens. Annals Academiae Scientiarium Fennicae series A 2:5–151.

Kappel F & JA Flore. 1983. Effects of shade on photosynthesis, specific leaf weight, leaf chlorophyll content, and morphology of young peach trees. Journal of the American Society of Horticultural Science 108:541–544.

Kershaw AP & MS McGlone. 1995. The Quaternary history of the southern conifers. In: The ecology of southern conifers. NJ Enright & RS Hill (eds.). Chapter 3: 30–63. Melbourne University Press. Carlton.

Kershaw K. 1973. Quantitative and dynamic plant ecology. 2nd edition. Edward Arnold. London.

Kilburn P. 1966. Analysis of species–area relation. Ecology 47(5):831–843.

King DA 1981. Tree dimensions: maximizing the rate of height growth in dense stands. Oecologia 51:351–356.

King DA. 1990. The adaptive significance of tree height. The American Naturalist 135:809–828.

Kitzberger T, TT Veblen & R Villalba. 1995. Tectonic influences on tree growth in northern Patagonia, Argentina: the roles of substrate stability and climatic variation. Canadian Journal of Forest Research 25:1684–1696.

Kitzberger T, TT Veblen & R Villalba. 1997. Climatic influences on fire regimes along a rain forest–to–xeric woodland gradient in northern Patagonia, Argentina. Journal of Biogeography 24:35–47.

Knapp R. 1984. Sample (relevé) areas (distribution, homogeneity, size, shape) and plot–less sampling. In: Sampling methods and taxon analysis in vegetation science. Handbook of vegetation science 4. R Knapp (ed.). Chapter 11:101–119. Junk. The Hague.

Kozlowski TT & SG Pallardy. 1997a. Physiology of woody plants. 2nd edition. Academic Press. San Diego.

Kozlowski TT & SG Pallardy. 1997b. Growth control in woody plants. Academic Press. San Diego.

Kramer PJ & JP Decker. 1944. Relation between light intensity and rate of photosynthesis of loblolly pine and certain hardwoods. Plant Physiology 19:350–357.

Kramer PJ & WS Clark. 1947. A comparison of photosynthesis in individual pine needles and entire seedlings at various light intensities. Plant Physiology 22:51–57.

Krebs C. 1959. Observaciones fenológicas sobre plantas indígenas del Parque Nacional Nahuel Huapi. Anales de Parques Nacionales 8:127–133.

Krebs Ch. 1989. Ecological methodology. Harper Collins. New York.

Kristensen NP & ES Nielsen 1983. The *Heterobathmia* life history elucidated: immature stages contradict assignment to suborder Zeugloptera (Insecta, Lepidoptera). Zeitung Zoologischer Systematik Evolforsen 21:101–124.

Krueger KW & RH Ruth. 1969. Comparative photosynthesis of red alder, Douglas–fir, Sitka spruce, and western hemlock seedlings. Canadian Journal of Botany 47:519–527.

Kuiper LC. 1994. Architectural analysis of Douglas–fir forests. PhD thesis. Wageningen Agricultural Unversity. Wageningen.

Labandeira CC & JJ Seproski. 1993. Insect diversity in the fossil record. Science 261:310–315.

LaMarche VC, RL Holmes, PW Dunwiddie & LG Drew. 1979. Tree–ring chronologies of the southern hemisphere. Vol.1: Argentina. Chronologies series V. Laboratory of Tree–Ring Research. University of Arizona. Tucson.

Lara A. 1991. The dynamics and dusturbance regimes of *Fitzroya cupressoides* forests in the south–central Andes of Chile. PhD thesis. University of Colorado. Boulder.

Lara A & R Villalba. 1993. A 3620–year temperature record from *Fitzroya cupressoides* tree rings in southern South America. Science 260:1104–1106.

Lara A, C Donoso & JC Aravena. 1995. La conservación del bosque nativo en Chile: problemas y desafíos. In: Ecología de los bosques nativos de Chile. JJ Armesto, C Villagrán & MK Arroyo (eds.). Chapter 18:335–362. Universitaria. Santiago de Chile.

Larcher W. 1980. Physiological plant ecology. 2nd edition. Springer–Verlag. Berlin.

Lassoie JP, TM Hinckley & CC Grier. 1985. Coniferous forests of the Pacific Northwest. In: Physiological ecology of northern American plant communities. BF Chabot & HA Mooney (eds.). Chapter 5:127–161. Chapman & Hall. New York.

Lebedeff N. 1942. Rejuvenecimiento del ciprés e influencia de la ganadería. Boletín Forestal 1938–40. Dirección General Parques Nacionales. Buenos Aires.

Legendre P & M Fortin. 1989. Spatial patterns and ecological analysis. Vegetatio 80:107–138.

Le Guin U. 1972. The word for world is forest. Minotauro. Barcelona.

Lennon JA, ES Martin & DL Wigston. 1982. A scanning electron microscope survey of leaf cuticules of some species of *Nothofagus* Bl. in the United Kingdom. Watsonia 14:312.

Le–Quesne CE. 1988. Caracterización de los bosques de ciprés de la cordillera (*Austrocedrus chilensis*) en Radal–7 Tazas, VII Región, Chile. Tesis de grado. Facultad de Ciencias Forestales. Universidad Austral de Chile. Valdivia.

Li HL. 1953a. A reclassification of *Libocedrus* and Cupressaceae. Journal of the Arnold Arboretum 34(1):17–36.

Li HL. 1953b. Present distribution and habitats of the conifers and taxads. Evolution 7:245–261.

Lidgard S & PR Crane. 1990. Quantitative analysis of the early angiosperm radiation. Nature 331:344–346.

Linder S & E Troeng. 1980. Photosynthesis and transpiration of 20–year old Scots pine. In: Structure and function of northern coniferous forests: an ecosystem study. T Persson (ed.). Ecological Bulletin 32:165–181. National Science Research Council. Stockholm.

Lloyd DG. 1982. Selection of combined versus separate sexes in seed plants. The American Naturalist 120(5):571–585.

Lloyd DG & CJ Webb. 1977. Secondary sex characters in plants. The Botanical Review 43:177–216.

Loehle C. 1988. Tree life history strategies: the role of defenses. Canadian Journal of Forest Research 18:209–222.

Loehle C. 1990. Proper statistical treatment of species–

area data. Oikos 57(1):143–145.

Lorimer C. 1985. Methodological considerations in the analysis of forest impact history. Canadian Journal of Forest Research 15:200–213.

Lucero M. 1996. Regeneración temprana del bosque de ciprés de la cordillera. Tesis de grado. Centro Regional Universitario Bariloche – Universidad Nacional del Comahue. Unpublished.

Lusk CH. 1996. Stand dynamics of the shade–tolerant conifers *Podocarpus nubigena* and *Saxegothaea conspicua* in Chilean temperate rain forest. Journal of Vegetation Science 7:549–558.

Lusk CH & J Odgen. 1992. Age structure and dynamics of a podocarp–broadleaf forest in Tongariro National Park, New Zealand. Journal of Ecology 80:379–393.

Macphail MK, GJ Jordan & RS Hill. 1993. Key periods in the evolution of the Cenozoic flora and vegetation of Tasmania 1: the early–middle Pleistocene. Australian Journal of Botany 41:673–707.

Magnuson JJ. 1990. Long–term ecological research and the the invisible present. BioScience 40:495–501.

Marchelli P & LA Gallo. 1999. Annual and geographic variation in seed traits of Argentinean populations of southern beech *Nothofagus nervosa* (Phil.) Dim.et Mil. Forest Ecology and Management 121:239–250.

Markgraf V. 1983. Late and postglacial vegetational and paleoclimatic changes in subantarctic, temperate and arid environments in Argentina. Palynology 7:43–70.

Markgraf V. 1987. Palaeoenvironmental changes at the northern limit of the subantarctic *Nothofagus* forests, lat.37°, Argentina. Quaternary Research 28:119–129.

Markgraf V. 1989. Reply to CJ Heusser's "Southern westerlies during the last glacial maximum". Letter to the editor. Quaternary Research 31:426–432.

Markgraf V. 1993. Climatic history of Central and South America since 18,000 yr BP: comparison of pollen records and model simulations. In: Global climates since the Last Glacial Maximum. HE Wright Jr., JE Kutzbach, T Webb III, WF Ruddiman, FA Street–Perrott & PJ Bartlein (eds.). University of Minnesota Press. Minneapolis.

Martin PG & JM Dowd. 1993. Using sequences of rbcL to study phylogeny and biography of *Nothofagus* species. Proceedings Southern Temperate Ecosystems. Origin and Diversification. Australian Systematic Botany 6(5):441–447.

Maynard Smith J. 1989. Evolutionary genetics. Oxford University Press. Oxford.

McGraw JB & K Garbutt. 1990. The analysis of plant growth in ecological and evolutionary studies. Trends in Ecology and Evolution 5(8):251–254.

McGregor WH & PJ Kramer. 1963. Seasonal trends in rates of photosynthesis and respiration in loblolly pine. American Journal of Botany 50:760–765.

McQueen DR. 1976. The ecology of *Nothofagus* and associated vegetation in South America. Part I. Tuatara 22(1):38–68.

McQueen DR. 1977. The ecology of *Nothofagus* and associated vegetation in South America. Part II. Tuatara 22(3):233–244.

Meagher TR. 1992. The quantitative genetics of sexual dimorphism in *Silene latifolia* (Caryophyllaceae). I. Genetic variation. Evolution 46:445–457.

Mercer J. 1976. Glacial history of southernmost South America. Quaternary Research 6(2):125–166.

Mercer J. 1984. Late Cainozoic glacial variations in South America south of the Ecuador. In: Late paleoclimates of the southern hemisphere. JC Vogel (ed.). pag.45–58. Balkema. Rotterdam.

Mermoz M & C Martín. 1987. Mapa de vegetación del Parque y la Reserva Nacional Nahuel Huapi. Administración de Parques Nacionales. Buenos Aires.

Midgley JJ & WJ Bond. 1991. How important is biotic pollination and dispersal to success of the angiosperms? Philosophical Transactions of the Royal Society of London B 333:209–215.

Miller A. 1976. The climate of Chile. In: Climates of Central and South America. W. Schwerdtfeger (ed.). World Survey of Climatology 12. Chapter 3:113–145. Elsevier. Amsterdam.

Miller CN. 1977. Mesozoic conifers. The Botanical Review 43(2):217–280.

Miller CN. 1988. The origin of modern conifer families. In: Origin and evolution of gymnosperms. CB Beck (ed.). Chapter 10: 448–504. Cambridge University Press. New York.

Miller RW & RL Donahue. 1995. Soils in our environment. 7th edition. Prentice Hall. New Jersey.

Mlincek D. 1991. The holistic concept of natural productive forests. Quaterly Journal of Forestry 85:8–11.

Mohler C, P Marks & D Sprugel. 1978. Stand structure and allometry of trees during self–thinning of pure stands. Journal of Ecology 66:599–614.

Moran P. 1950. Notes on continuous stochastic phenomena. Biometrika 37:17–23.

Moravec J. 1973. The determination of the minimal area of phytocenoses. Folia Geobotanica et Phytotaxonomica 8:23–47.

Morisita M. 1959. Measuring the dispersion of individuals and analysis of the distributional patterns. Memoirs Faculty of Sciences Kyushu University. Series E. 2:215–235.

Mueller–Dombois D & H Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons. New York.

Müller–Using B & F Schlegel. 1981. The development of seedlings of Chilean *Nothofagus* species in a shaded area. Plant Research and Development 12:152–184.

Muñoz M. 1993. Algunos antecedentes sobre propagación de *Nothofagus*. Ciencia e Investigación Forestal 7(2):377–389.

Murúa R & LA González. 1985. Producción de semillas de especies arbóreas en la pluviselva valdiviana. Bosque 6(1):15–23.

Muttarelli E & E Orfila. 1971. Algunos resultados de las investigaciones de manejo silvicultural que se realizan en los bosques andino–patagónicos de Argentina. Revista Forestal Argentina 17(3):69–75.

Nambiar EK & R Sands. 1993. Competition for water and nutrients in forests. Canadian Journal of Forest Research 23:1955–1968.

Neave IA, JO Dawson & EH DeLucia. 1989. Autumnal photosynthesis is extended in nitrogen–fixing European black alder compared with basswood; possible adaptive significance. Canadian Journal of Forest Research 19:12–17.

Nelson ND. 1984. Woody plants are not inherently low in photosynthetic capacity. Photosynthetica 18:600–605.

Nelson ND, DI Dickmann & KWGottschalk. 1982. Autumnal photosynthesis in short–rotation intensively cultured *Populus* clones. Photosynthetica 16:321–333.

Newell EA. 1991. The direct and delayed costs of reproduction in *Aesculus californica*, the California buckeye tree. Journal of Ecology 79:365–378.

Nixon KC. 1989. Origins of Fagaceae. In: Evolution, systematics, and fossil history of the Hamamelidae. Vol.2: "Higher" Hamamelidae. PR Crane & S.Blackmore (eds.), p.23–43. Systematics Association Special Volume 40B. Clarendon. Oxford.

Norton DA, JG Palmer & J Odgen. 1987. Dendroecological studies in New Zealand. 1. An evaluation of tee age estimates based on increment cores. New Zealand Journal of Botany 25:373–383.

Odgen J, CH Lusk & MG Steel. 1993. Episodic mortality, forest decline and diversity on a dynamic landscape: Tongariro National Park, New Zealand. In: Forest decline in the Atlantic and Pacific regions. RF Huettl & D Mueller–Dombois (eds.), pp.261–274. Springer. Berlin.

Odgen J & GH Stewart. 1995. Community dynamics of the New Zealand conifers. In: The ecology of southern conifers. NJ Enright & RS Hill (eds.). Chapter 5: 81–119. Melbourne University Press. Carlton.

Oldeman RAA. 1978. Architecture and energy exchange of dicotyledonous trees in the forest. In: Tropical trees as living systems. PB Tomlinson & MH Zimmermann (eds.). Chapter 23:535–560. Cambridge University Press. Cambridge.

Oldeman RAA. 1983. Tropical rain forests, architecture, silvigenesis and diversity. In: Tropical rain forests: ecology and management. SL Sutton, TC Whitmore & AC Chadwick (eds.). p.139–150. Blackwell. Oxford.

Oldeman RAA. 1990. Forests: elements of silvology. Springer–Verlag. Berlin.

Oldeman RAA & J van Dijk. 1991. Diagnosis of the temperament of tropical rain forest trees. In: Rain forest regeneration and management. A Gómez–Pompa, TC Whitmore & M Hadley (eds.). MAB series vol.6. Chapter 2:21–65. UNESCO–Parthenon. Paris.

Oldeman RAA & AHM Sieber–Binnenkamp. 1994. Timber trees: architecture and ecology. In: Tropical trees: the potential for domestication and the rebuilding of forest resources. RRB Leakey & AC Newton (eds.). ITE Symposium 29:25–33. HMSO. London.

Oliver CD. 1981. Forest development in North America following major impacts. Forest Ecology and Management 3:153–168.

Oliver CD & BC Larson. 1996. Forest stand dynamics. Updated edition. John Wiley & Sons. New York.

Ordóñez A. 1987. Germinación de tres especies de *Nothofagus* siempreverdes (coigües) y variabilidad en la germinación de procedencias de coigüe común (*Nothofagus dombeyi*, (Mirb.) Oerst.). Tesis de grado. Facultad de Ciencias Forestales. Universidad Austral de Chile. Valdivia.

Ovington JD. 1956. The form, weight and productivity of tree species grown in close stands. New Phytologist 55:289–304.

Ovington JD. 1960. The accumulation of energy in forest plantations in Britain. Journal of Ecology 48:639–

646.

Oyama K & R Dirzo. 1988. Biomass allocation in the dioecious tropical palm *Chamaedorea tepejilote* and its life history consequences. Plant Species Biology 3:27–33.

Pardé J & J Bouchon. 1988. Dendrométrie. 2nd edition. Ecole Nationale du Genie Rural, dex Eaux et des Forêts (ENGREF). Nancy.

Pearson AK, OP Pearson & IA Gómez. 1994. Biology of the bamboo *Chusquea culeou* (Poaceae: Bambusoideae) in southern Argentina. Vegetatio 111:93–126.

Peet R & N Christensen. 1987. Competition and tree death. BioScience 37(8):586–595.

Persson R. 1974. World forest resources. Review of the world's forest resources in the early 1970's. Research Note 17. Department of Forest Survey. Institutionen för Skogstaxering. Royal College of Forestry. Stockholm.

Peterken GF. 1996. Natural woodland. Ecology and conservation in northern temperate regions. Cambridge University Press. Cambridge.

Peters R. 1997. Beech forests. Geobotany series 24. Kluwer. Dordrecht.

Philipson WR & MN Philipson. 1979. Leaf vernation in *Nothofagus*. New Zealand Journal of Botany 17:417–421.

Philipson WR & MN Philipson. 1988. A classification of the genus *Nothofagus* (Fagaceae). Botanical Journal of the Linnean Society 98:27–36.

Pickett STA & PS White (eds.). 1985. The ecology of natural impact and patch dynamics. Academic Press. New York.

Pielou E. 1977. Mathematical ecology. 2nd edition. John Wiley & Sons. New York.

Piñero D, J Sarukhan & P Alberdi. 1982. The costs of reproduction in a tropical palm, *Astrocaryum mexicanum*. Journal of ecology 70:473–481.

Pita JC. 1931. El crecimiento del ciprés (*Libocedrus chilensis* End.). Centro Nacional de Ingenieros Agrónomos. Buenos Aires.

Pollard DFW & PF Wareing. 1968. Rates of dry–matter production in forest tree seedlings. Annals of Botany 32:573–591.

Poole AL. 1987. Southern beeches. Information Series 162. DSIR, Science Information Publishing Centre. Wellington. New Zealand.

Poorter H, C Remkes & H Lambers. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. Plant Physiology 94:621–627.

Popp JW & IA Reinhartz. 1988. Sexual dimorphism in biomass allocation and clonal growth of *Xanthoxylum americanum*. American Journal of Botany 75: 1732–1741.

Porter SC, M Stuiver & CJ Heusser. 1984. Holocene sea–level changes along the Strait of Magellan and Beagle Channel, southernmost South America. Quaternary Research 22:59–67.

Rabassa J & C Clapperton. 1990. Quaternary glaciations of the southern Andes. Quaternary Science Review 9:153–174.

Radosevich SR & JS Holt. 1984. Weed ecology: implications for vegetation management. John Wiley & Sons. New York.

Ramírez C, H Figueroa & J San Martin. 1988. Comportamiento ecosociológico de los *Nothofagus* sudamericanos. Monografías de la Academia Nacional de Ciencias Exactas, Físicas y Naturales 4:55–61. Buenos Aires.

Raunkiaer C. 1934. The life forms of plants. Clarendon. Oxford.

Raven PH. 1977. A suggestion concerning the Cretaceous rise to dominance of the angiosperms. Evolution 31:451–452.

Read J & RS Hill. 1985. Photosynthetic responses to light of Australian and Chilean species of *Nothofagus* and their relevance to the rainforest dynamic. New Phytologist 101:731–742.

Read J & RS Hill. 1988. The dynamics of some rainforest associations in Tasmania. Journal of Ecology 76:558–584.

Read J, GS Hope & RS Hill. 1990. Integrating historical and ecophysiological studies in *Nothofagus* to examine the factors shaping the development of cool rainforest in southeastern Autralia. In: Proceedings 3rd IOP Conference. Melbourne, 1988. JG Douglas & DC Christophel (eds.). Pag.97–106. A–Z Printers. Melbourne.

Rebertus AJ & TT Veblen. 1993. Structure and tree–fall gap of old–growth *Nothofagus* forests in Tierra del Fuego, Argentina. Journal of Vegetation Science 4:641–654.

Regal PJ. 1977. Ecology and evolution of flowering plant dominance. Science 196:622–629.

Reich PB, MB Walter & Ellsworth. 1992. Leaf lifespan in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs 62:365–392.

Reich PB, K Takayoshi, ST Gower & AW Schoettle. 1995. Causes and consequences of variation in conifer leaf life–span. In: Ecophysiology of coniferous forests. WK Smith & TM Hinckley (eds.). Chapter 8:225–254. Academic Press. San Diego.

Relva MA & TT Veblen. Impacts of introduced large herbivores on *Austrocedrus chilensis* forests in northern Patagonia, Argentina. Forest Ecology and Management. In press.

Retallack G & DL Dilcher. 1981. A coastal hypothesis for the dispersal and rise to dominance of flowering plants. In: Paleobotany, paleoecology, and evolution. KJ Niklas (ed.). pp. 27–67. Praeger. New York.

Rodríguez G. 1990. Propagación de *Nothofagus* chilenos por medio de semillas. Agro–Ciencia 6(2):119–122.

Rodríguez García D, A Sourrouille, G Gallopín & C Montaña. 1978. Estudio ecológico integrado de la cuenca del río Manso Superior. II.Tipos de vegetación. Anales de Parques Nacionales 14:231–240.

Roig FA, JA Boninsegna & RL Holmes. 1992. Growth rates in diameter, basal area and height of *Pilgerodendron uviferum*; relationship between growth index and germination. Trees, Structure and Function 6:199–203.

Romero EJ. 1980. Arquitectura foliar de las especies sudamericanas de *Nothofagus* Bl. Boletín de la Sociedad Argentina de Botánica 19 (1–2):289–308.

Romero EJ. 1986. Fossil evidence regarding the evolution of *Nothofagus* Bl. Annals of the Missouri Botanical Garden 73:276–283.

Romero EJ. 1988. Momentos importantes en la evolución de Nothofagus Bl. Monografías de la Academia Nacional de Ciencias Exactas, Físicas y Naturales 4:15–23. Buenos Aires.

Rosenfeld JM. 1972. Desarrollo de la regeneración de raulí (*Nothofagus alpina*) y coigüe (*Nothofagus dombeyi*) bajo diferentes grados de luminosidad. Tesis de grado. Facultad de Ingeniería Forestal. Universidad Austral de Chile. Valdivia.

Rossignol M, L Rossignol, RAA Oldeman & A Ambroise. 1998. Struggle of life or the natural history of stress and adaptation. Treemail. Heelsum.

Rothkugel M. 1916. Los bosques patagónicos. Ministerio de Agricultura de la Nación. Buenos Aires.

Rovere AE. 1991. Estudio experimental de la germinación y el desarrollo temprano del ciprés de la cordillera. Tesis de grado. Centro Regional Universitario Bariloche. Universidad Nacional del Comahue. Unpublished.

Rush V. 1992. Principales limitantes para la regeneración de la lenga en la zona NE de su área de distribución. Publicación Técnica 8:61–73. CIEFAP–GTZ. Esquel.

Sakai A & N Oden. 1983. Spatial patterns of sex expression in silver maple (*Acer saccharinum* L.): Morisita's index and spatial autocorrelation. The American Naturalist 122(4):489–508.

Salwasser H. 1994. Ecosystem management: can it sustain diversity and productivity? Journal of Forestry 92(8):6–10.

Sancholuz LA, S Calí, R Albariño & P Guerrero. 1993. ¿Crecen más los machos que las hembras del ciprés de la cordillera? Proceedings 16th Congreso de la Sociedad Argentina de Ecología. Puerto Madryn.

Sancholuz LA, A Rovere & M Lucero. Los bosques de *Austrocedrus chilensis*: producción de semillas, semillas viables y germinación. Unpublished.

San Martín J & C Donoso. 1995. Estructura florística e impacto antrópico en el bosque Maulino de Chile. In: Ecología de los bosques nativos de Chile. JJ Armesto, C Villagrán & MK Arroyo (eds.). Chapter 8:153–168. Universitaria. Santiago de Chile.

Santelices R, M Riquelme & F Rojas. 1996. Aspectos sobre la semilla y germinación de *Nothofagus glauca* (Phil.) Kasser de dos procedencias de la VII Región. Ciencia e Investigación Forestal 10(2). En prensa.

Satoo T & HA Madgwick 1982. Forest biomass. Martinus Nijhoff. The Hague.

Schmaltz J. 1991. Deciduous forests of southern South America. In: Ecosystems of the world. E Röhrig & B Ulrich (eds.), p.557–578. Elsevier. Amsterdam.

Schmithüsen J. 1960. Die Nadelhölzer in den Waldgesellschaften der südlichen Anden. Vegetatio 9:313–327.

Schultze ED, MI Fuchs & M Fuchs. 1977. Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest in northern Germany. I. Biomass distribution and daily CO_2 uptake in different crown layers. Oecologia 29:43–61.

Schweingruber FH. 1993 Trees and woods in dendrochronology. Springer–Verlag. Berlin.

Seibert P. 1982. Carta de vegetación de la región de El Bolsón y su aplicación a la planificación del uso de la tierra. Fundación para la Educación, la Ciencia y la Cultura. Buenos Aires.

Seneca. ca.50. In: Perlin J. 1991. A forest journey: the role of wood in the development of civilization. Harvard University Press. Cambridge.

Serra M, R Gajardo & A Cabello. 1985. Ficha técnica de especies amenazadas. CONAF/Universidad de Chile. Santiago de Chile.

Seymour RS & ML Hunter, Jr. 1999. Principles of ecological forestry. In: Maintaining biodiversity in forest ecosystems. ML Hunter, Jr. (ed.). Chapter 2:22–61. Cambridge University Press. Cambridge.

Shannon CE & M Weaver. 1949. The mathematical theory of communication. University of Illinois Press. Urbana.

Shea M, P Dixon & R Sharitz. 1993. Size differences, sex ratio, and spatial distribution of male and female water tupelo, *Nyssa aquatica* (Nyssaceae). American Journal of Botany 80(1):26–30.

Silvertown JW & J Lovett Doust. 1993. Introduction to plant population biology. Blackwell. Oxford.

Singer P. 1971. Forest mycology and forest communities in South America. II. Mycorrhiza sociology and fungus succession in the *Nothofagus dombeyi* – *Austrocedrus chilensis* woods of Patagonia. U.S. Department of Agriculture. Miscellaneous Publication 1189:204–215.

Sionit N, BR Strain, H Hellmers, GH Riechers & CH Jaeger. 1985. Long–term atmospheric CO_2 enrichment afffects the growth and development of *Liquidambar styraciflua* and *Pinus taeda* seedlings. Canadian Journal of Forest Research 15:468–471.

Six Dijkstra H. 1981. Architecture and age structure of terrace rimu forest at Saltwater, South Westland, New Zealand. MSc. thesis. University of Canterbury. New Zealand.

Smith DM, BC Larson, MJ Kelty & PM Ashton. 1997. The practise of silviculture: applied forest ecology. 9th edition. John Wiley & Sons. New York.

Sneath PHA. 1967. Conifer distribution and continental drift. Nature 215:467–470.

Sokal R & N Oden. 1978. Spatial correlation in biology. I. Methodology. Biological Journal of the Linnean Society 10:199–228.

Spies TA & JF Franklin. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific northwest. Ecology 70:543–545.

Stebbins GL. 1981. Why are there so many species of flowering plants? Bioscience 31:573–577.

Stearns SC. 1992. The evolution of life histories. Oxford University Press.

Stokes M & T Smiley. 1968. An introduction to tree–ring dating. University of Chicago Press. Chicago.

Swanson FJ & RE Sparks. 1990. Long–term ecological research and the invisible place. BioScience 40: 502–508.

Swanson FJ & JF Franklin. 1992. New forestry principles from ecosystem analysis of Pacific Nortwest Forests. Ecological Applications 2(3):262–274.

Taylor DW & LJ Hickey. 1996. Evidence for and implications of an herbaceous origin for angiosperms. In: Flowering plants origin, evolution and phylogeny. DW Taylor & LJ Hickey (eds.). Chapter 9:232–266. Chapman & Hall. New York.

Theophrastus. ca.300 BC. In: Readings in ecology. EJ Kormondy (ed.). Prentice–Hall. Englewoods Cliffs.

Thomas SC & JV LaFrankie. 1993. Sex, size, and interyear variation in flowering among dioecious trees of the Malayan rain forest. Ecology 74:1529–1537.

Thomasson K. 1959. Nahuel Huapi: plankton of some lakes in an Argentine National Park, with notes on terrestrial vegetation. Acta Phytogeographica Suecica 42:1–83.

Thorne RF. 1983. Proposed new realignements in the angiosperms. Nordic Journal of Botany 3:85–117.

Thorne RF. 1992. Classification and geography of the flowering plants. The Botanical Review 58: 225–348.

Tiffney BH. 1984. Seed size, dispersal syndromes and the rise of angiosperms: evidence and hypothesis. Annals of the Missouri Botanical Garden 71:551–576.

Tilman D. 1997. Mechanisms of plant competition. In: Plant ecology. MJ Crawley (ed.). Chapter 8:239–261. Blackwell. Oxford.

Tolley LC & BR Strain. 1984. Effects of CO_2 enrichment on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings under different irradiance levels. Canadian Journal of Forest Research 14:343–354.

Tortorelli L. 1947. Los incendios de bosques en la Argentina. Ministerio de Agricultura de la Nación. Buenos Aires.

Tortorelli L. 1956. Maderas y bosques argentinos. Acme. Buenos Aires.

Tranquilini W. 1962. Beitrag zur Kausalanalyse des Wettbewerbs ökologisch verschiedener Holzarten. Deutschland Botanische Gesellschaft 75:353–364.

Tuley G. 1980. *Nothofagus* in Britain. 2nd edition. Forestry Commission. Forest Record 122:1–26. London.

Upton C & B Flingleton. 1985. Spatial data analysis by example. Vol.1: Point pattern and quantitative data. John Wiley & Sons. New York.

USDA. 1975. Soil taxonomy. Soil Survey Staff. Agricultural Handbook 436. United States Department of Agriculture. Washington.

Usher M. 1975. Analysis of pattern in real and artificial plant populations. Journal of Ecology 63:569–586.

van der Hout 1999. Reduced impact logging in the tropical rain forests of Guyana. Tropenbos–Guyana series 6. Tropenbos–Guyana Programme. Georgetown.

van Rompaey RSAR. 1993. Forest gradients in West Africa: a spatial gradient analysis. PhD thesis. Wageningen Agricultural University. Wageningen.

van Steenis CGGJ. 1953. Results of the Archibold Expeditions: Papuan *Nothofagus*. Journal of the Arnold Arboretum 34:300–374.

van Steenis CGGJ. 1954. Additional note on *Nothofagus*. Journal of the Arnold Arboretum 35:266–267.

Vasiliauskas S & L Aarssen. 1992. Sex ratio and neighbor effects in monospecific stands of *Juniperus virginiana*. Ecology 73(2): 622–632.

Veblen TT. 1982. Growth patterns of *Chusquea* bamboos in the understorey of Chilean *Nothofagus* forests and their influences in forest dynamics. Bulletin of the Torrey Botanical Club 109(4):474–487.

Veblen TT. 1987. *Nothofagus* regeneration in treefall gaps in northern Patagonia. Canadian Journal of Forest Research 19:365–371.

Veblen TT. 1989. Tree regeneration responses to gap in a transandean gradient. Ecology 70(3):541–543.

Veblen TT. 1992. Regeneration dynamics. In: Plant succession: theory and prediction. D Glenn–Lewin, RK Peet & TT Veblen (eds.). Chapter 4:153–187. Chapman & Hall. New York.

Veblen TT & DH Ashton. 1978. Catastrophic influences on the vegetation of the Valdivian Andes. Vegetatio 36(3):149–167.

Veblen TT, DH Ashton & FM Schlegel. 1979. Tree regeneration strategies in a lowland *Nothofagus*–dominated forest in south–central Chile. Journal of Biogeography 6:329–340.

Veblen TT, F Schlegel & B Escobar. 1980. Structure and dynamics of old–growth *Nothofagus* forests in the Valdivian Andes, Chile. Journal of Ecology 68:1–31.

Veblen TT, C Donoso, FM Schlegel & R Escobar. 1981. Forest dynamics in south–central Chile. Journal of Biogeography 8:211–247.

Veblen TT, FM Schlegel & JV Oltremari. 1983. Temperate broad–leaved evergreen forests of South America. In: Temperate broad–leaved forests. JD Ovington (ed.). Chapter 2:5–31. Elsevier. Amsterdam.

Veblen TT & DC Lorenz. 1987. Post–fire stand development of *Austrocedrus – Nothofagus* forests in northern Patagonia. Vegetatio 71:113–126.

Veblen TT & DC Lorenz. 1988. Recent vegetation changes along the forest / steppe ecotone of northern Patagonia. Annals Association of American Geographers 78(1):93–111.

Veblen TT, DH Ashton, S Rubulis, D Lorenz & M Cortés. 1989a. *Nothofagus* stand development on in–transit moraines, Casa Pangue Glacier, Chile. Artic Alpine Research 21:144–155.

Veblen TT, M Mermoz, C Martín & E Ramilo. 1989b. Effects of exotic deer on forest regeneration and composition in northern Patagonia. Journal of Applied Ecology 26:711–724.

Veblen TT, T Kitzberger & A Lara. 1992a. Impact and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. Journal of Vegetation Science 3:507–520.

Veblen TT, M Mermoz, C Martín & T Kitzberger. 1992b. Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. Conservation Biology 6(1):71–83.

Veblen TT & PB Alaback. 1996. A comparative review of forest dynamics and impact in the temperate rainforests of North and South America. In: High latitude rain forests and associated ecosystems of the west coast of America. RG Lawford, PB Alaback & ER Fuentes (eds.). Chapter 9:173–213. Springer–Verlag. New York.

Veblen TT, RS Hill & J Read. 1996 (eds.). The ecology and biogeography of *Nothofagus* forests. Yale University Press. New Haven.

Veblen TT, T Kitzberger, R Villalba & J Donnegan. 1999. Fire history in northern Patagonia: the roles of humans and climatic variations. Ecological Monographs 69(1):47–67.

Veit H & K Garleff. 1995. Evolución del paisaje cuaternario y los suelos en Chile central–sur. In: Ecología de los bosques nativos de Chile. JJ Armesto, C Villagrán & MK Arroyo (eds.). Chapter 2:29–49. Universitaria. Santiago de Chile.

Vestal A. 1949. Minimum areas for different vegetations: their determination from species–area curves. Biological Monographs 20(3):1–129.

Vester HFM. 1997. The trees and the forests: the role of tree architecture in canopy development. A case study in secondary forests (Araracuara, Colombia). PhD thesis. Wageningen Agricultural University. Wageningen.

Villagrán C. 1990. Glacial climates and their effects on the history of the vegetation of Chile: a synthesis based on palynological evidence from northern Isla de Chiloé. Review of Palaeobotany and Palynology 65:17–24.

Villalba R. 1990. Climatic fluctuations in northern Patagonia during the last 1,000 years as inferred from tree-ring records. Quaternary Research 34:346–360.

Villalba R & TT Veblen. 1997a. Spatial and temporal variation in *Austrocedrus* along the forest-steppe ecotone in northern Patagonia. Canadian Journal of Forest Research 27:580–597.

Villalba R & TT Veblen. 1997b. Regional patterns of tree population age structures in northern Patagonia: climatic and impact influences. Journal of Ecology 85:113–124.

Villalba R & TT Veblen. 1998. Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. Ecology 79(8):2624–2640.

Wagner RG & JC Zasada. 1991. Integrating plant autoecology and silvicultural activities to prevent forest vegetation management problems. The Forestry Chronicle 67(5):506–513.

Walter H. 1977. Zonas de vegetación y clima. Omega. Barcelona.

Wardle P. 1983. Temperate broad–leaved evergreen forests of New Zealand. In: Temperate broad–leaved forests. JD Ovington (ed.). Chapter 3:33–71. Elsevier. Amsterdam.

Waring R & WH Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press. Orlando.

Watt AS. 1947. Pattern and process in the plant community. Journal of Ecology 35:1–22.

Weiner J. 1990. Asymmetric competition in plant populations. Trends in Ecology and Evolution 5(11):360–364.

Welch HJ. 1991. The conifer manual. Vol.1. Kluwer. Dordrecht.

Westhoff V & E van der Maarel. 1978. The Braun–Blanquet approach. In: Classification of plant communities. RH Whittaker (ed.). pag.287–399. Junk. The Hague.

Whipple S. 1980. Population dispersion patterns of trees in a southern Lousiana hardwood forest. Bulletin of the Torrey Botanical Club 107(1):71–76.

Whittaker RH. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47:103–121.

Wiegleb G. 1989. Explanation and prediction in vegetation science. Vegetatio 83:17–34.

Williamson G. 1975. Pattern and seral composition in an old–growth beech–mapple forest. Ecology 56:727–731.

Willis B. 1914. El norte de Patagonia. Naturaleza y riquezas. Tomo 1. Comisión de Estudios Hidrológicos. Ministerio de Obras Públicas. Buenos Aires.

Wilson EO. 1993. Forest ecosystems: more complex than we know. In: Defining sustainable forestry. Aplet G, N Johnson, JT Olson y VA Sample (eds). Foreword:11–13. Island Press. Washington.

Woodward FI. 1995. Ecophysiological controls of conifer distributions. In: Ecophysiology of coniferous forests. WK Smith & TM Hinckley (eds.). Chapter 4:79–94. Academic Press. San Diego.

WRI. 1986. An assessment of the resource base that supports the global economy. World Resource Institute (WRI). New York.

Wright CA. 1965. The volcanic ash soils of Chile. Report to the Government of Chile. Report 2017. Food and Agricultural Organization (FAO). Rome.

Wright SJ & CP van Schaik. 1994. Light and the phenology of tropical trees. The American Naturalist 143:192–199.

Zobel B & JP van Buijtenen. 1989. Wood variation. Springer–Verlag. New York.

Acknowledgments

I gratefully acknowledge to Prof. Roelof A.A.Oldeman (Wageningen University and Research Centre, WUR) for his commitment during the supervision of the present study. He generously shared his ideas and time, and allowed me to have a thoughtful academic experience at WUR.

I am also indebted to Prof. Luis A.Sancholuz (Universidad Nacional del Comahue, UNC), who co-supervised this study and always encouraged me to continue my education.

This study would have been impossible without the vital support of my family, to whom this text is dedicated as a scanty testimony of my deep gratitude.

The following persons deserve my recognition for kindly assisting me during the different instances of this project: Ismael Andía, Susana Antoliche, Nora Baccalá, Cecilia Brión, Salvador Calí, Pablo Cortondo, Ezequiel Dezzotti, Wiert Dijkkamp, Virginia Fontana, Mario Gentili, Fiore Grasso, Dennis Jansen, Wyb Jonkers, Cristina Lozada, Carlos Lozada, Uriel Mele, Hernán Mattes, Martín Naumann, Pablo Pérez, Horacio Planas, Javier Puntieri, Andrea Relva, Pedro Temporetti, Sascha van der Sleesen, Begoña Vento, and Fernando Zaretti.

I also appreciate the collaboration given by the staff of Hutan Lestari International (WUR) Dela Boeijink, Marthy Boudewijn, and Ed de Bruijn.

I am grateful to many professors and lecturers mainly from UNC and WUR, who gave me the scientific background for improving my understanding of complex entities such as natural forests.

I express sincere thanks to the Asentamiento Universitario at San Martín de los Andes (AUSMA) for granting me institution privileges, exempting to carry out my regular activities during my stay at WUR.

I acknowledge to Nahuel Huapi National Park authorities to permit collecting data within the natural reserve.

Anonymous referees provided constructive criticisms to different parts of the study.

The essential financial support was provided by The Netherlands Fellowship Programme and Wageningen University and Research Centre in The Netherlands, and the Universidad Nacional del Comahue (Centro Regional Universitario at San Carlos de Bariloche and Asentamiento Universitario at San Martín de los Andes) in Argentina.

Curriculum vitae

Alejandro Dezzotti was born in San Carlos de Bariloche (Argentina) on December 26, 1963. In 1989 he received a degree in Biology from Universidad Nacional del Comahue (UNC, Argentina). Between 1992 and 1994 he attended a postgraduate programme in Forest Ecology and Silviculture, receiving a MSc. degree from Wageningen University and Research Centre University (WUR, The Netherlands). During the last three years, he has followed a PhD programme at WUR. At present, he is a full-time permanent member of UNC at San Martín de los Andes. He is lecturer in Ecology and Biology courses for forestry students, and researcher in projects concerning the regenerative ecology of mixed Nothofagus forests and the assessment of environmental impacts.