Forest Ecology and Management 176 (2003) 87–103

Forest Ecology and Management

www.elsevier.com/locate/foreco

Stand structure and dendroecology of an old-growth *Nothofagus* forest in Conguillio National Park, south Chile

William Pollmann[*]

Institute of Landscape Ecology, Westfälische Wilhelms-Universität Münster, Robert-Koch-Strasse 26, D-48149 Münster, Germany

Received 30 May 2001; received in revised form 4 February 2002; accepted 10 May 2002

Abstract

The regeneration pattern and dynamics of two emergent southern beech trees (*Nothofagus alpina*, *Nothofagus dombeyi*) were inferred from population age structure and spatial patterns in a forest dominated by the deciduous *N. alpina* in Conguillio National Park, south Chile. Diameter–frequency, diameter–age relations, and analysis of radial growth patterns of *N. alpina* (‘‘raulí’’) and evergreen *N. dombeyi* (‘‘coihue’’) were examined at a montane elevation site in the Andean Range. The present age structure indicates that the oldest *N. alpina* established before 1463 and the oldest *N. dombeyi* between 1480 and 1520. The forest was uneven-aged as were the populations of raulí and coihue. *N. alpina* dominated the overstory layer, with few *N. dombeyi* dominant trees, and had fairly continuous recruitment between 1463 and 1984. Since 1885, tree recruitment in the forest has been dominated by both *N. alpina* and *N. dombeyi*. The master tree-ring chronology of *N. alpina* exhibited abrupt growth changes from 1650 to 1725. Increased growth rates occurred after a major volcanic explosion of Volcan Llaima around 1640, followed by a relatively sharp decline in growth from 1730 to 1850; growth remained high from the 1850s to the 1990s. Releases in radial growth, indicative of moderate- and small-scale disturbances occurred in most of the oldest trees during the last 400 years. Multiple periods of release and suppression indicate that *N. alpina* may take advantage of gaps to reach the main canopy. Gap turnover times in this *N. alpina*–*N. dombeyi* forest were estimated at >500 years, although gap formation was highly episodic and possibly associated with regionally strong windstorms, volcanic activity, and stand-level dieback. Gap and treefall characteristics in the forest are similar to results from other mixed *Nothofagus* forests in northern Patagonia, southern Chile and Tierra del Fuego. As the vegetation of the surveyed forest was homogenous over the last five centuries, it is concluded that regeneration and coexistence of long-lived *Nothofagus* spp. depends primarily on fine- and moderate-scale single treefall gaps.

Keywords: Long-lived pioneer species; *Nothofagus*; Regeneration pattern; Forest dynamics; Temperate rainforest

1. Introduction

The study of tree-ring chronologies from old-growth forests has greatly improved our understanding of stand dynamics and tree species coexistence (Fritts and Swetnam, 1989; Abrams and Copenheaver, 1999). There have been numerous studies of ecological history of forests in terms of population dynamics, species recruitment patterns, periodicity and intensity of disturbance (such as wind, fire, volcanism, and insect outbreaks), impact of climate, and successional dynamics (e.g. Veblen et al., 1981, 1999; Frelich and Graumlich, 1994; Abrams et al., 1995; Villalba and Veblen, 1997; Freléchoux et al., 2000; Fujita and Sano, 2000). Studying tree-ring chronologies coupled

---

[*] Tel.: +49-251-8330060; fax: +49-251-8338352.
E-mail address: pollmaw@uni-muenster.de (W. Pollmann).

PII: S0378-1127(02)00279-7

with stand and age structures, land-use history, climatic data, and ecological attributes of individual species has proven to be a particularly strong approach for understanding long-term forest dynamics (Orwig and Abrams, 1994; Abrams et al., 1998; Ruffner and Abrams, 1998).

The northern Wintero-Nothofagetea region, where deciduous *Nothofagus alpina* (Poepp. et Endl.) Oerst. forms an altitudinal belt on montane elevation sites, is distributed in the major part of the cool-temperate zone with winter-rainfall in southern South America (Oberdorfer, 1960; Eskuche, 1999; Pollmann, 2001). In this area, the stand and age structures, and regeneration process of mixed old-growth *Nothofagus betuloides–N. pumilio* forests were studied by many scientists (Gutiérrez et al., 1991; Veblen et al., 1992; Rebertus and Veblen, 1993a,b; Rebertus et al., 1993); however, there have been only few studies in *N. alpina* forests under steady-state conditions.

N. alpina is a broad-leaved deciduous species known to be the most competitive species along with laurophyllous tree species (such as *Laurelia philippiana*, *Aextoxicon punctatum*, *Persea lingue*) and small-leaved evergreen *Nothofagus dombeyi*, respectively (Pollmann, 2001). Generally, *N. alpina* is a light-demanding tree (Donoso, 1993; Veblen et al., 1996), and grows rapidly in height when favorable conditions occur (Read and Hill, 1985; Donoso et al., 1993). Being a pioneer species in the submontane belt, *N. alpina* often replaces laurophyllous tree species (e.g. *L. philippiana*) as a dominant species following large-scale disturbances (Veblen et al., 1979a, 1980). In the Valdivian Andes, the longevity of *Nothofagus* spp. and the frequency of periodic catastrophic disturbances promoted *Nothofagus*-dominated forests replaced by *Laurelia–Aextoxicon* climax forests (Veblen et al., 1981; Veblen, 1985a). Many studies suggest that large-scale disturbances and treefall gap dynamics favored *Nothofagus*-dominated forests (cf. Veblen et al., 1996). In southern Chile, frequency and intensity of canopy disturbances have been assessed by age structure and by using radial growth analysis, and tree species population dynamics at stand and landscape scales in many forests (Brun, 1969; Müller-Using, 1973; Veblen et al., 1977a, 1979a, 1980, 1992; Veblen and Ashton, 1978; Uebelhör, 1984; Veblen, 1985a, 1989a; Donoso et al., 1993; Rebertus and Veblen, 1993a,b; Rebertus et al., 1993; Lusk, 1996a,b, 1999). However, few studies have examined the succession and forest development in pure *N. alpina–N. dombeyi* stands at higher altitudes in south-central Chile, where no laurophyllous trees occur.

In this study, a 535-year history of species recruitment and dendroecology for an old-growth *N. alpina–N. dombeyi* forest at the Conguillio National Park in south-central Chile is reported. The specific objectives of the study are: (1) to quantify the present composition and structure of the forest, (2) to describe on the long-term patterns of species recruitment and radial growth variation, (3) to investigate the impacts of natural and anthropogenic disturbances on the long-term forest dynamics, and (4) to come to an understanding of the forest history and successional status of the stand. The results of the study will improve our understanding of the ecology, dynamics, and succession of old-growth mixed *Nothofagus* forests in southern South America. For nomenclature, see Marticorena and Quezada (1985).

2. Methods

2.1. Study area

The study site is located at 1200 m a.s.l. in the Conguillio National Park surrounding Volcan Llaima (38°38′20″S, 71°36′30″W, 3125 m a.s.l.) in the Andean Range, southern Chile (Fig. 1). Volcan Llaima originated during the Pleistocene and its base is from the Tertiary Age. Parent rocks are igneous, such as granits, diorits and andesits (Clapperton, 1993). Large expanses of lava flows attest the activity of Volcan Llaima. More than 40 eruptions occurred since 1852 (Casertano, 1963; Moreno and Varela, 1985). The soils are classified as andosols being derived from either pyroclastic deposits or lava; these young soils lack a well-developed structure and consist of thin organic horizons only (Besoaín, 1985; Veit and Garleff, 1995). Mean annual precipitation is 2500–3000 mm. The relatively high elevations of the park result in a cool climate. The mean monthly maximum temperature at 100 m a.s.l. (at Temuco weather station, the nearest weather observatory to the study site) is highest in January (15.1 °C) and lowest in July (7.6 °C). Snow falls from May to September and

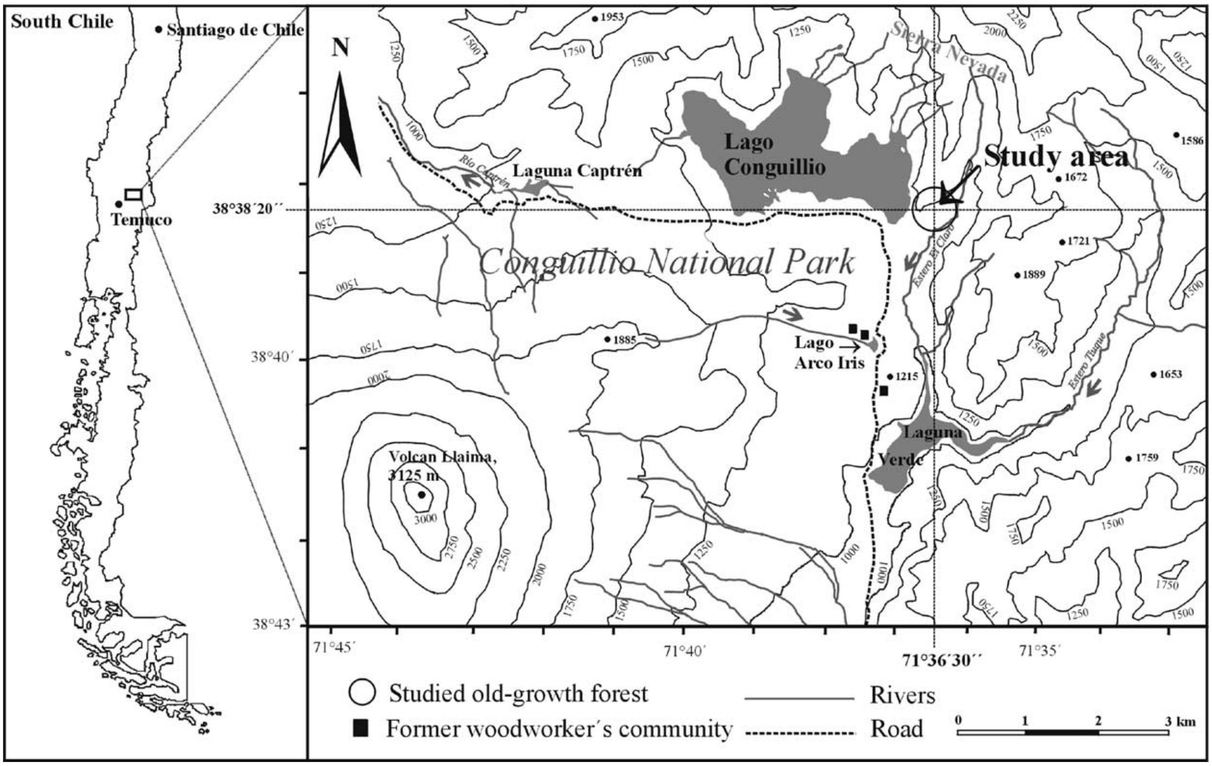

Fig. 1. Study site near Volcan Llaima in the Conguillio National Park, southern Chile.

reaches a depth of 200–300 cm from June to August (Miller, 1976). As to temperature and rainfall regime, the area belongs to the mesotemperate bioclimatic belt and the humid ombrotype (Amigo and Ramírez, 1998).

N. alpina forests occur between 900 and 1300 m a.s.l. in the Conguillio National Park. However, they are now rare below 1000 m a.s.l. because of human land use (Gajardo, 1994). Phytosociologically, the forests are classified as Nothofagetum dombeyi-alpinae (Pollmann, 2001). Bamboo such as *Chusquea culeou* dominate the understory of the stand. Within the Chilean forest type system, the forest belongs to the "*N. obliqua*–*N. alpina*–*N. dombeyi*" type (Donoso, 1981). Near the study site, there was a woodworker's community some 250 years ago. First settlers selectively harvested *N. alpina* for material woods, and seeds of *Araucaria araucana* as food while occupying the banks of the Estero El Claro (Martin, 1923; Fig. 1). In 1927 they moved out, when a lava flow from a parasitic cone of Volcan Llaima created Lago Arco Iris (Casertano, 1963). There were two or three families only. Although the extent and frequency of cutting was unclear, they likely cut a few middle or large size trees for regional uses. Throughout the Conguillio National Park, the effects of human disturbance such as cutting or fires can be observed in form of denuded slopes, standing dead trees, and intensively regenerating second-growth forests. The fires (mainly caused by humans) originated in the valleys, sweeping up-slope causing damage that appears as inverted-V shape on the affected ridges. In addition, along the entrance road to the park at lower elevations (~900 m a.s.l.) the effects of recent fire, livestock grazing, and the substitution of native forests by plantations of exotic trees (such as *Pinus radiata*, *Pseudotsuga menziesii*, *Eucalyptus globulus*) can be seen. There was no human disturbance (such as fire and selective logging) after 1950, when the Volcan Llaima area was designated as a National Park (Torres and Torres, 1998). Old-growth characteristics such as large diameter trees, a variety of diameter classes and canopy layers, gap formation, and coarse woody debris on the forest floor are common to the forest in the studied area (Sierra Nevada, Fig. 1). However, evidence of windthrow and past fires from charring on several trees was observed; cut stumps from past logging were not observed at the study site.

2.2. Field survey

On March 1999, a structure plot of 40 m × 30 m (0.12 ha) in the center of the *N. alpina* community was used for vegetation and dendroecological sampling (Schweingruber, 1996). Criteria for selection of this plot were homogeneous patterned vegetation and enough trees (>10 overstory trees) for dendroecological investigations (Rigling and Schweingruber, 1997). Classification of tree crowns into three categories (dominant, codominant, suppressed) was based on the amount and direction of intercepted light (Smith et al., 1997). A profile diagram and crown projection map were made of all recorded trees in the 0.12 ha section (see Lamprecht, 1980 for methods). Within the plot area of 1200 m^2 all trees ($\geq$5.0 cm dbh) were counted and mapped. Species, height, and diameter (at breast height; 1.37 m) were recorded. The tree species were cored (two perpendicular cores were taken at the base cross section) for age determination and radial growth analysis, whereas small trees were cut and sliced at their root collar. All cores and cross-sections were dried, sanded, and examined (cf. Iseli and Schweingruber, 1989; Leuschner, 1994; Schweingruber, 1996).

2.3. Data and radial growth analysis

For each tree species, a relative importance value was calculated as an average of the relative frequency, relative density, and relative dominance based on basal area (Cottam and Curtis, 1956; Abrams et al., 1998). In total, 73 samples were aged using a binocular microscope. For most trees, procedures described in Norton et al. (1987) and Duncan (1989) were used to estimate the number of missing rings for cores that did not include the chronological center of the tree, but represented at least 70% of the geometric radius. No correction was applied for time required to grow to coring height (Abrams et al., 1998; Lusk, 1999). Analysis of annual growth increments followed an accuracy of 0.01 mm using Time Series Analysis and Presentation (TSAP©) program (Rinn, 1996). Annual increment series for each tree were skeleton-plotted and cross-dated using event years (Fritts, 1976; Schweingruber, 1996; Lorimer et al., 1999). A ring width index (RWI) was created for each individual tree chronology by dividing yearly measured growth values by the expected values obtained from linear regression (Fritts, 1976; Fritts and Swetnam, 1989). After crossdating, ring width indices were averaged to obtain a mean growth chronology from cores per species (*N. alpina*, *N. dombeyi*). All cores ($n = 21$) were examined for periods of suppression and release based on conservative and moderate criteria established by Lorimer and Frelich (1989), who defined a major sustained release as a $\geq$100% average growth increase lasting at least 15 years, and a moderate temporary release as a >50% average growth increase lasting from 10 to 15 years. In this study, frequency of major and moderate releases, mean RWI, and tree establishment dates were used to distinguish disturbance events and forest regeneration dynamics.

3. Results

3.1. Stand structure

The stand structure and tree species-composition indicated that the contemporary forest overstory is dominated by deciduous *N. alpina* (“raulí”) (Fig. 2). The high importance of raulí was due to its high basal area and moderate frequency, whereas the importance of *N. dombeyi* (“coihue”) was due primarily to its moderate density (Table 1). Average stand density of 451 trees ha^{-1} and average stand area of 89.47 m^2 ha^{-1} are somewhat smaller than that reported for other primeval *Nothofagus* forests in southern Chile (e.g. Veblen et al., 1996; CONAF, 1998), but within the expected range for mixed *N. alpina*–*N. dombeyi* forests (Donoso and Lara, 1998). *N. alpina* represented 62.9% of the total importance value.

The diameter distribution of trees exhibited a roughly negative exponential or inverse-J pattern typical of uneven-aged forests (Fig. 3; Smith et al., 1997). *N. alpina* dominated the larger diameter classes and was poorly represented among the middle diameter classes from 21 to 60. *N. dombeyi* occurred in almost every class with diameter <60 cm, but was best

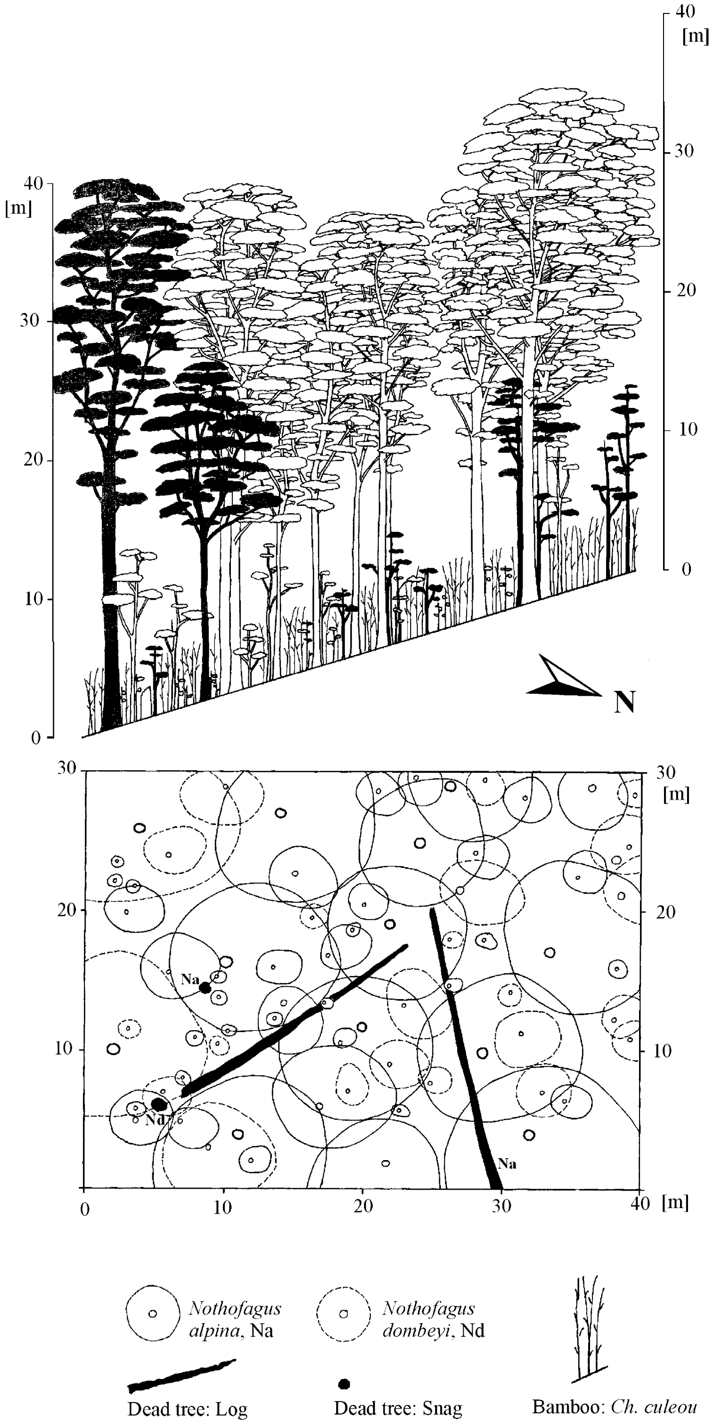

Fig. 2. Transect showing the structure and different phases of development. Above is a profile diagram and below is a crown projection map of the studied plot (outer boundary of 40 m × 30 m; evergreen *N. dombeyi* trees are colored in black while the deciduous *N. alpina* trees remain white).

Table 1
Frequency, density and basal area, and dominance (relative importance value) for tree species in an old-growth *N. alpina*–*N. dombeyi* forest at Conguillio National Park, south Chile

	N. alpina	*N. dombeyi*	Total
Frequency (no. in plot)[a]	37	21	58
Density (trees ha^{-1})[a]	253.7	197.3	451.0
Basal area (m^2 ha^{-1})[a]	63.3	26.1	89.5
Relative density (%)	56.3	43.7	100
Relative frequency (%)	61.6	38.4	100
Relative basal area (%)	70.8	29.2	100
Relative importance value (%)	62.9	37.1	100

[a] Individuals > 10 cm dbh.

represented in the smaller classes (5–30 cm diameter); coihue also occurred in the larger diameter classes. *N. alpina* is most important in the dominant class as is evident from the canopy class distribution (Fig. 4). Both *N. alpina* and *N. dombeyi* are common tree species in the codominant and suppressed classes; however, raulí occurred most frequently among the suppressed trees with diameter <10 cm.

3.2. Age structure

The age data from all samples ($n = 73$) and recruitment history at the study site suggested an uneven age of the forest (Fig. 5). *N. alpina* exhibited continuous establishment since 1725 with peak numbers in the 1950s. In the stand, intensive tree establishment continued for at least 100 years between the 1870s and the 1970s. Unfortunately, heart rot was very prevalent in many of the larger and older *N. alpina* and *N. dombeyi* trees, which limited the ability to age what may have been some of the older trees in the stand (cf. Lusk, 1999). Gap turnover times in the *N. alpina*–*N. dombeyi* forest were estimated at >500 years, although gap formation was highly recurrent and possibly associated with regionally extensive windstorms, volcanic activity, and stand-level dieback (Veblen et al., 1996). The oldest tree present in the stand was a 535-year-old *N. alpina* (Fig. 6). All other trees in the forest were ≤500 years old, except for a 509-year-old *N. alpina*. Raulí had fairly continuous recruitment between 1463 and 1984 (Fig. 6). On the other hand, *N. dombeyi* reproduced irregularly before

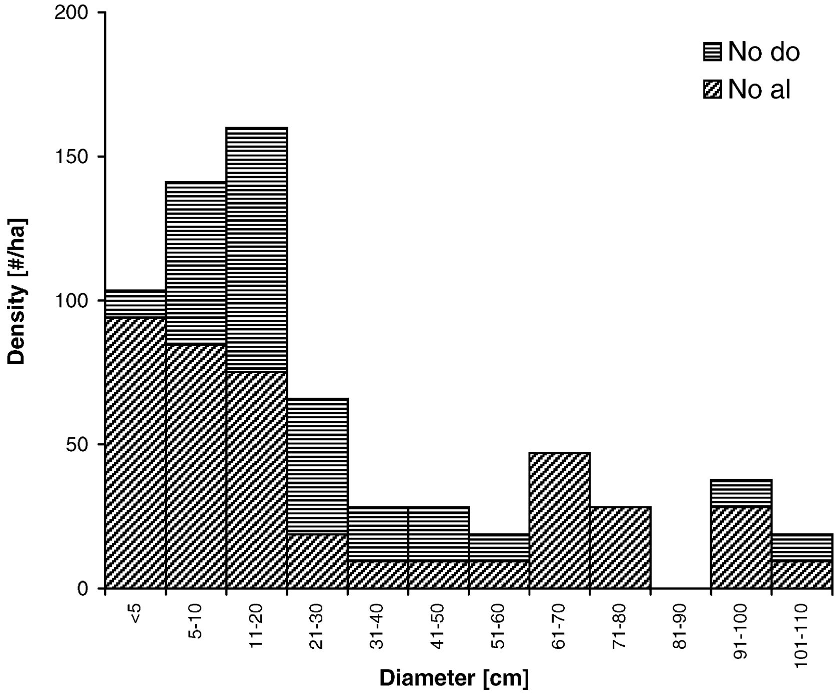

Fig. 3. Diameter (at 1.37 m) distribution of tree species in an old-growth *N. alpina*–*N. dombeyi* forest at Conguillio National Park in southern Chile.

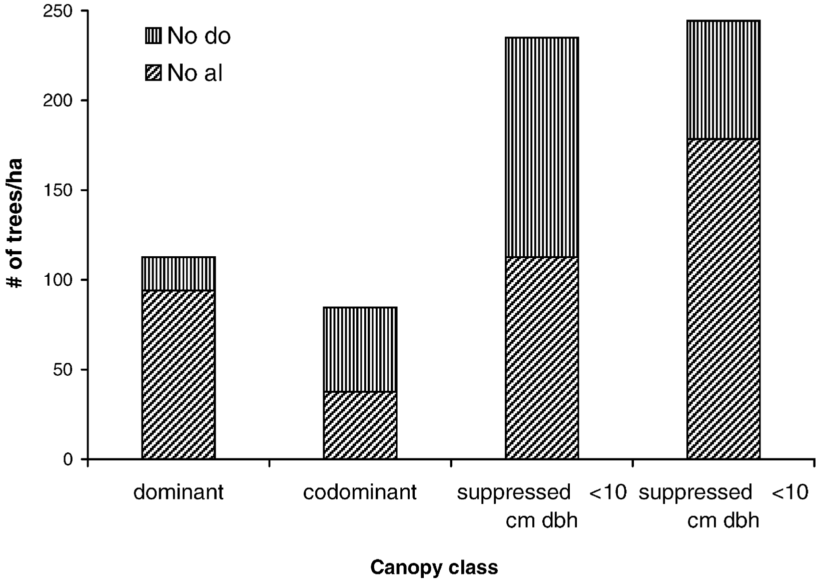

Fig. 4. Canopy class distribution of tree species in an old-growth *N. alpina*–*N. dombeyi* forest at Conguillio National Park, Chile.

1741, but more continuously after 1885. The majority of aged coihue trees (85%, $n = 28$) entered the population during the 19th and 20th century (since 1885); only four trees cored were older than 250 years, and only two of these were older than 500 years (Fig. 6).

3.3. Developmental processes

The radial growth pattern showed a strong positive relationship with reported forest disturbances, with most *N. alpina* trees showing major growth releases after large-scale canopy openings. For example, the master tree-ring chronology comprising the ten oldest *N. alpina* trees in the forest exhibited an increase in growth rates from 1650 to 1725, released from abrupt growth changes after the major volcanic explosion of Volcan Llaima around 1640, indicative of extensive canopy openings throughout the stand (Fig. 6). Growth then decreased sharply from 1730 to 1850. *N. alpina* trees, however, were consistently suppressed. Between the 1850s and the 1990s growth remained high with much year-to-year variation and *N. alpina* trees might have reached canopy layer. A similar analysis for *N. dombeyi* revealed some differences with the *N. alpina* chronology (Fig. 6). Growth in the oldest *N. alpina* was high and fluctuated around the mean increment $(\mathrm{RWI} = 1)$ during the last 250 years; between 1960 and 1995, the RWI increased considerably resulting in some of the highest RWI values during the last 250 years. It is likely that the dramatic growth variation in some *N. alpina* trees during that period were due to an interaction of disturbance-caused damage to trees and openings in the canopy layer (Foster, 1988; Rebertus and Veblen, 1993a; Abrams and Orwig, 1995). However, after 1880, the recruitment of tree species evenly was not clear associated with releases in either the *N. alpina* or *N. dombeyi* chronology (Fig. 6).

Radial growth pattern and release dates of individual trees varied among and within the two *Nothofagus* species (Figs. 7 and 8). *N. alpina* and *N. dombeyi* trees showed marked differences in growth histories, with differences in radial growth releases for each of the trees, which indicates that each tree was influenced mainly by moderate- and small-scale disturbances that had local impacts on the forest during the last 400 years (cf. Schweingruber et al., 1990a, 1991; Schweingruber, 1996). *N. alpina* growth rates varied from 0.09 mm per year (Fig. 7F) to 4.18 mm per year (Fig. 7D and H). Average growth was 1.04 mm per year. In comparison, *N. dombeyi* trees had maximum growth rates of 4.54 mm per year (Fig. 8B) and minimum growth of 0.15 mm per year (Fig. 8A), while the average was 1.16 mm per year.

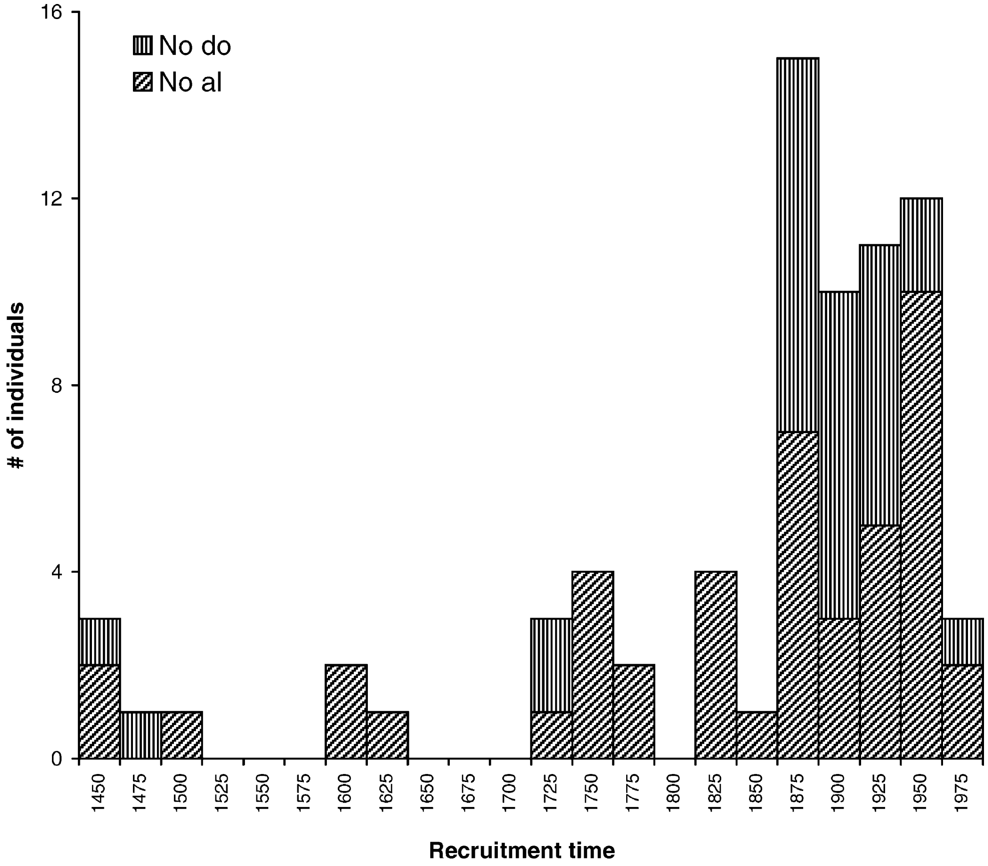

Fig. 5. Age class distribution of tree species in the old-growth forest.

There were some substantial intraspecific differences in radial growth patterns and releases. For example, the 535-year-old *N. alpina* exhibited moderate growth rates, ranging from 0.4 to 2.0 mm per year, with much year-to-year variation (Fig. 7A). Another *N. alpina* tree had an initial growth <0.6 mm per year and a major release in 1668, followed by declining growth the next 300 years, except in 1865 when growth was 2.44 mm per year (Fig. 7B). Abrupt growth changes and prolonged periods of suppressed growth were also found in other *N. alpina* chronologies. For example, a 362-year-old tree (Fig. 7E) exhibited a 200-year period of growth suppression < 0.61 mm per year, followed by a major release in 1845. The annual increment of a 360-year-old tree (Fig. 7F) fell below 0.35 mm per year in the 1720s and below 0.11 mm per year in the 1750s. A major release did not occur before 1861. Other *N. alpina* exhibited moderate rather then declining growth rates, followed by its maximum rates of 2.78 and 4.18 mm per year, respectively, after a major release in 1850 (Fig. 7C and D). A 218-year-old dominant raulí had an initial growth exceeding 2.7 mm per year, followed by four decades of declining growth (Fig. 7G); since 1820 the annual increment in this tree varied between 0.8 and 3.66 mm per year, with much year-to-year variation. A similar pattern was reported for another relatively young dominant *N. alpina* (Fig. 7H) that had high initial growth (2.64 mm per year). During the next 75 years growth decreased. The annual increment in this tree fell below 1.0 mm per year (in 1799, 0.44 mm per year), until moderate releases in 1839, 1863, 1878, and 1890. All *N. alpina* chronologies presented in Fig. 7 were from dominant and codominant canopy trees. Among these trees, growth similarities were found for only a few pointer years. Thus, event

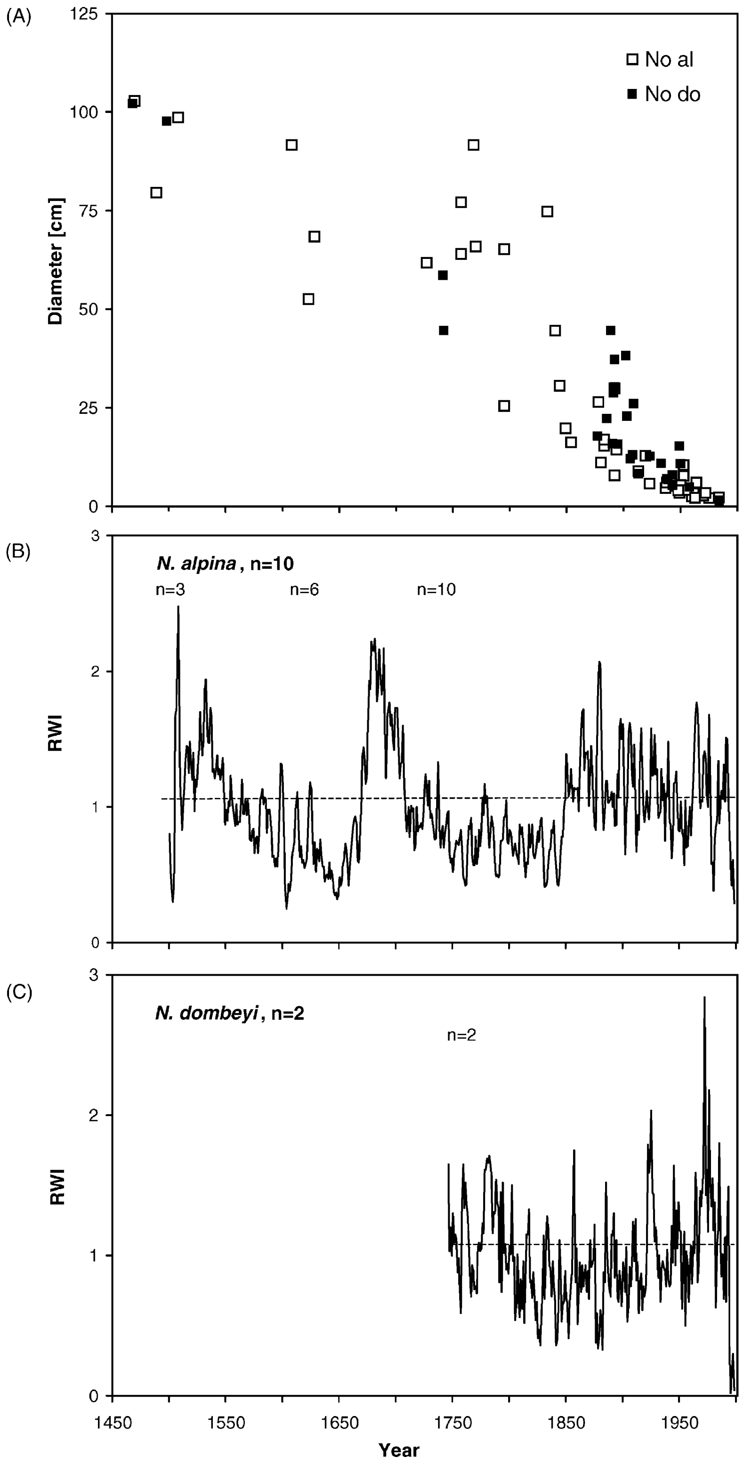

Fig. 6. Age–diameter data for all cored trees (A) and the mean RWI for the oldest *N. alpina* (B) and oldest *N. dombeyi* (C) in the old-growth forest.

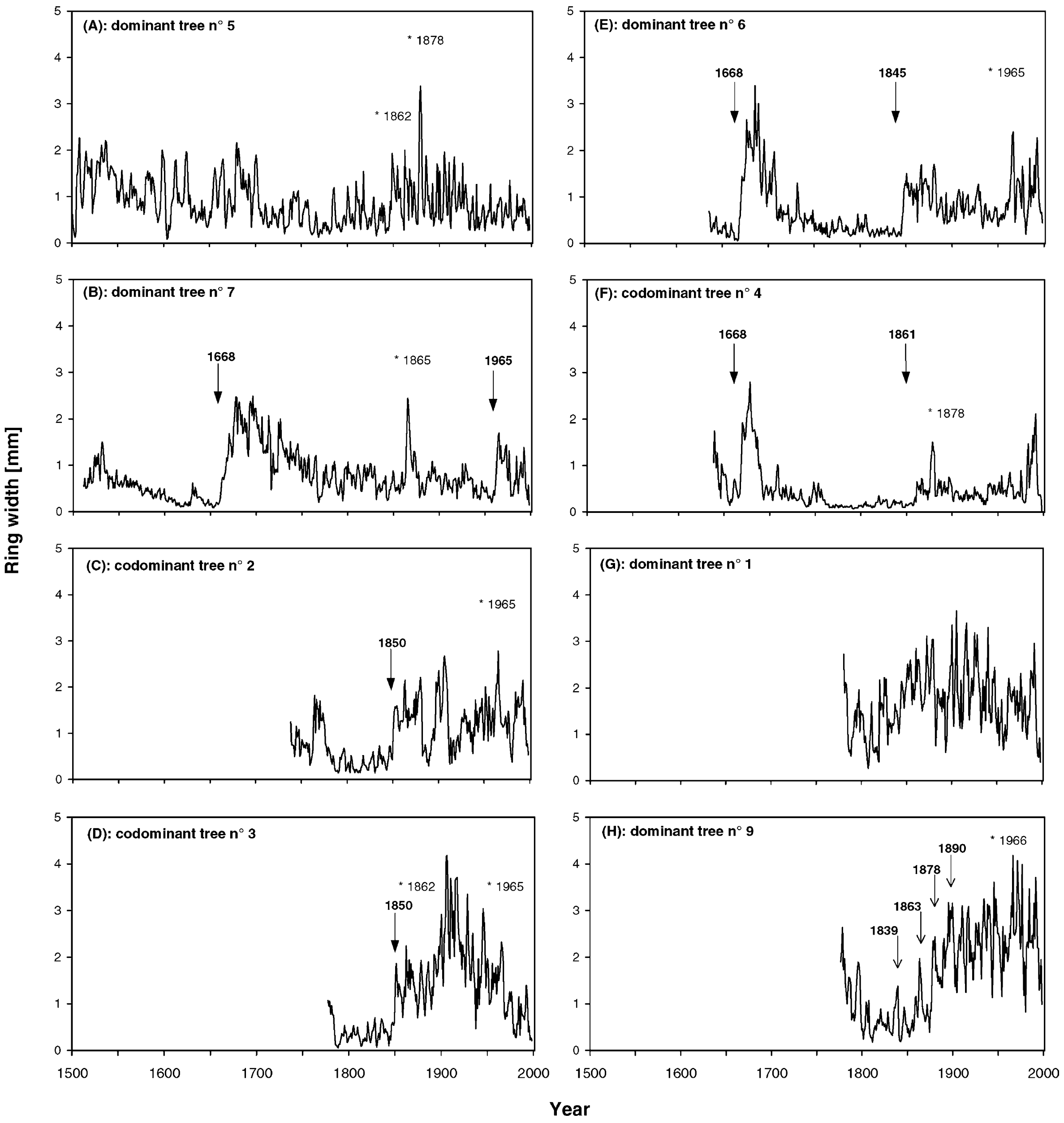

Fig. 7. Radial growth chronologies of selected *N. alpina*. Black arrows: major release dates; arrows: moderate release dates (based on conservative and moderate criteria established by Lorimer and Frelich, 1989); ∗: event years (calculated for the present study using the methods given in Schweingruber et al., 1990b; Schweingruber, 1996).

years (sensu Schweingruber et al., 1990b; Schweingruber, 1996) were identified and quantified on the basis of abrupt growth changes and ring width. For example in the 19th and 20th century, the single tree increment of *N. alpina* for which the skeleton-plot was available, there were some common positive reactions apparent. Some of these reactions were reflected in different chronologies: 1862, 1878, and 1965 (Fig. 7).

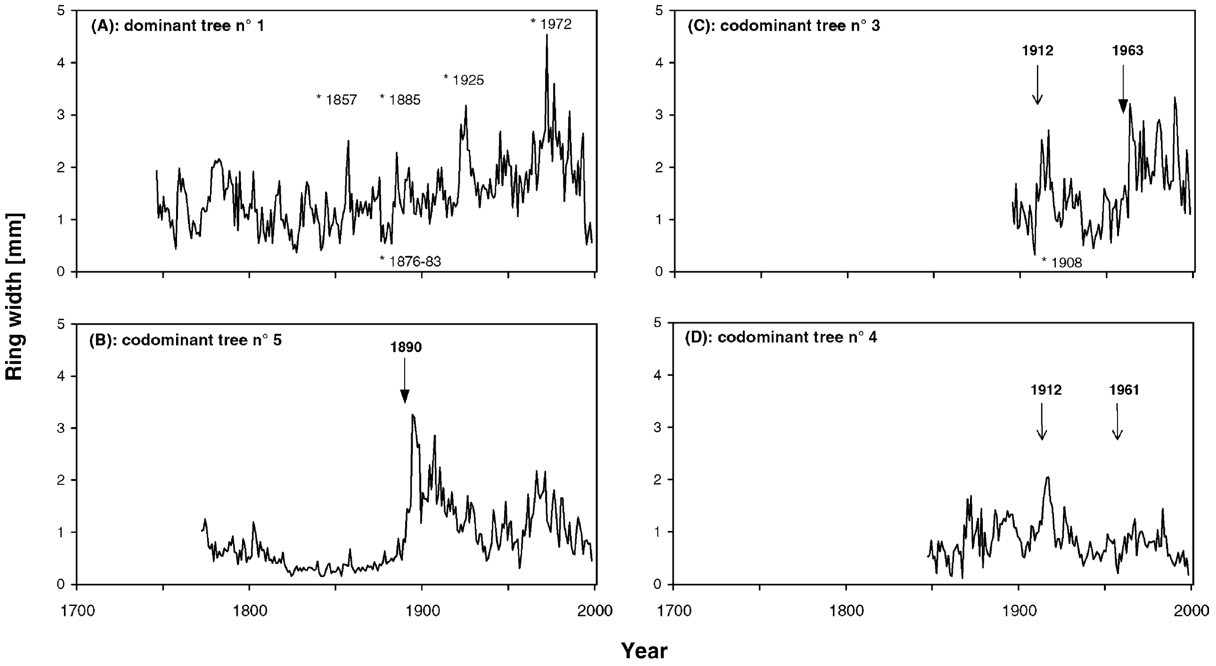

Fig. 8. Radial growth chronologies of selected *N. dombeyi*. Black arrows: major release dates; arrows: moderate release dates (based on conservative and moderate criteria established by Lorimer and Frelich, 1989); ∗: event years (calculated for the present study using the methods given in Schweingruber et al., 1990b; Schweingruber, 1996).

Likewise, most *N. dombeyi* showed striking differences in single tree radial growth patterns. An approximately 500-year-old dominant *N. dombeyi* had maximum growth rates >4.5 mm per year and minimum growth <0.5 mm per year, and exhibited significant releases or severe growth depression between 1750 and 1998 (Fig. 8A). For example, the annual increment of the tree fell below 0.9 mm per year in the 1870s until a moderate release in 1883. Positive event years were analyzed in 1857, 1925, and 1972. A 225-year-old codominant coihue had an initial growth of 1.25 mm per year. Then growth declined for more than a century to <0.4 mm per year. A major and moderate release followed in 1890 (>3.21 mm per year) and in 1965, respectively (Fig. 8B) that triggered the growth of this tree into the upper forest canopy. The codominant *N. dombeyi* tree no. 3 (Fig. 8C) had an initial growth rate >1.3 mm per year and a moderate release in 1912. This tree had a relatively short period of suppressed growth prior to a canopy accession release in 1963 when growth exceeded 2.5 mm per year, and probably started life in a treefall gap into the forest canopy without any significant understory suppression. A similar pattern was reported for this species in another codominant tree (Fig. 8D), but showed a moderate release in 1961 followed by a declining growth during the next 25 years. The annual increment in this tree was less than 0.5 mm in 1986, but without release, which suggests that it has been suppressed by more dominant trees from 1920 through 1998.

4. Discussion

N. alpina at this study site exhibited continuous recruitment between 1463 and 1984, and presently shares overstory dominance with *N. dombeyi*, this is in contrast to the lack of recent canopy recruitment of *N. alpina* in mid-elevation, transitional forests that contain *N. alpina* in combination with various laurophyllous species (cf. Veblen and Ashton, 1978; Veblen et al., 1980, 1981, 1996; Veblen, 1985b; Pollmann et al., 2000). The *N. alpina* component in the stand is therefore uneven-aged, which is unusual for this species (Veblen et al., 1996). For example, in a

N. alpina–L. philippiana–Saxegothaea conspicua forest at mid-elevations (600–1000 m a.s.l.) in the Province of Valdivia, *N. alpina* were of same age due to massive past disturbances, mainly landslides and volcanic eruptions (Veblen et al., 1980, 1981). It was suggested that without periodic natural catastrophes shade-tolerant *L. philippiana* and *S. conspicua* would replace shade-intolerant *Nothofagus*. The forest would return to a purely laurophyllous climax. However, in other Valdivian *N. alpina–N. dombeyi–L. philippiana–S. conspicua* forests, the *N. alpina* component was of different age following recruitment in moderate treefall gaps after disturbance by windstorms (Burschel et al., 1976; Uebelhör, 1984). In steady-state forests in southern Chile, *N. alpina* existed via occasional gap-capture but was a very minor component of the stands (Kalela, 1941; Oberdorfer, 1960; Brun, 1969, 1975; Uebelhör, 1984). The persistence of *N. alpina* and *N. dombeyi* at my study site indicates that the community is not clearly successional to a regional climax, e.g. *L. philippiana–S. conspicua* forest.

At higher elevations in the Andes, above the upper altitudinal limit of the shade-tolerant trees (>1000 m a.s.l.), the dynamics of the pure *Nothofagus* forests are also very likely influenced by massive disturbances (e.g. volcanic eruptions, mass movements, snow avalances) which lead to the formation of extensive even-aged stands (Veblen et al., 1981, 1996). In pure, old-growth *Nothofagus* spp. stands showing no sign of recent large-scale exogenous disturbances since the establishment of the oldest trees, Veblen et al. (1981) observed tree regeneration in gap phases creating a mosaic of even-aged patches of trees in these *Nothofagus* forests near timberline. However, the uneven-aged structure and the continuous occurrence of *N. alpina* at my study site indicate that the community is close to a steady-state vegetation, which assumes long-term stability of site maintaining a relatively stable species-composition and structure (cf. Whittaker, 1975; Peterken, 1996). Many present-day *N. alpina* forests in southern South America (Chile and Argentina) are considered to be caused by cutting and fire during the last at least two centuries and are now, after the anthropogenic disturbance ceased, returning to later successional forests of the Valdivian rainforest type (Veblen et al., 1981, 1996; Donoso, 1993; Frank and Finckh, 1999). This is not the situation for this steady-state forest. It seems likely that the key to understanding the coexistence and competition of *N. alpina* with *N. dombeyi* codominants are the light and disturbance factors at the site. This is a high elevation forest, above the upper altitudinal limit of laurophyllous trees. It is intriguing to find typically sclerophyllous shrubs such as *Maytenus magellanica*, *M. chubutensis*, *Pseudopanax laetevirens*, *Berberis trigona*, and the small-leaved evergreen tree *N. dombeyi* growing on this site. The distribution patterns of evergreen shrubs and coexistence of microphyllous *N. dombeyi* in this forest, may be explained by site properties, in particular by low minimum temperatures and the duration of snow cover (Weinberger, 1973; Seibert, 1996). Along latitudinal and altitudinal gradients in south Chilean forests, there is a gradual retreat of the evergreen foliage from the upper tree layer to the shrub layer (Hildebrand-Vogel, 2002); the ecological mechanism driving this seems to be temperature (cf. Woodward, 1987). However, the relatively high growth rates and large size of *N. alpina* is consistent with the idea of generally favorable growing conditions in the forest (Donoso et al., 1993). Indeed, a gradient analysis of habitats of *Nothofagus* forest types in southern Chile confirmed that *N. alpina* was associated with deep relatively nutrient-rich soils (Weinberger, 1973; Pollmann, 2001).

Because of better light conditions compared to the *N. alpina* forest with laurophyllous species (Pollmann et al., 2000), light-demanding *Nothofagus* spp. have very likely persisted as dominants in this forest due to continuous regeneration and establishment. Small- and moderate-scale disturbance frequency has probably supported the recruitment. The relatively high density of *Nothofagus* spp. saplings at the study site is comparable to other *N. alpina–N. dombeyi* stands in southern South America (Finckh, 1996; Eskuche, 1999; Pollmann, 2001). *N. alpina* is known to replace itself with stump sprouts following the top-killing of the tree (Veblen et al., 1996); *N. dombeyi* seedlings often establish on large decayed logs and elevated root buttresses (Veblen et al., 1981; Donoso, 1993). In addition, the dense cover of understory bamboo (*Chusquea* spp.) and litter cover reduce the ability of both *Nothofagus* species to establish vast numbers of seedlings found abundantly where the bare mineral soil has been exposed (Burschel et al., 1976). The presented dendroecological data suggest that *N. alpina* and *N. dombeyi* may invade gaps even at low seedling density. However, this is rather speculative because past *N. alpina* canopy recruitment are compared with present-day regeneration intensity (cf. Abrams and Copenheaver, 1999). Anyway, if the current regeneration is representative of the past 400–500 years, the ability of *N. alpina* to fill gaps in the presence of dense *N. alpina*–*N. dombeyi* forests is intriguing, and probably related to the impact of small- to moderate-scale disturbances on the forest floor (e.g. by treefall or ash deposition) and rapid growth under canopy gaps.

Disturbances occurred frequently in this steady-state forest studied, with as many as one to nine trees exhibiting major sustained or moderate temporary growth releases during the last 500 years. The oldest *N. alpina* I aged was 535 years (with a dbh of 103 cm). In an old-growth *N. alpina*–*N. dombeyi* forest in the Valdivian Province, *N. alpina* reached 126 cm dbh and were more than 650 years old (Pollmann, unpublished data). However, the maximum longevity of *N. alpina* may exceed 700–800 years (Brun, 1969). It is important to note that many *N. alpina* and *N. dombeyi* trees in the forest show extremely individual histories in increment due to environmental conditions, and radial growth rates are highly variable, so it is difficult to generalize about growth environments, such as canopy openings and competition. However, in this forest, single tree release data indicate that most of the actual dominant *Nothofagus* usually experiences a severe growth depression before attaining canopy status. Interspecifically, multiple periods of release and suppression indicate that both *N. alpina* and *N. dombeyi* appear to have taken advantage of gap events to reach the main canopy (Figs. 7 and 8). Treefall gaps occurred throughout the forest, and occasionally blow downs were observed, including some larger *N. alpina* and *N. dombeyi*. This implies the existence of an uneven-aged pattern of *Nothofagus* tree populations in the forest.

Given the proximity of the study site to the Volcan Llaima (Fig. 1), it is highly probable that periodic events of volcanic ash deposition (cf. Casertano, 1963) might play an important role in the maintenance of the mixed *N. alpina*–*N. dombeyi* forests in Conguillio National Park. For example, the data of the present study indicate growth releases after the major volcanic explosion of Volcan Llaima in ca. 1640. In addition, more than 40 eruptions of Volcan Llaima since 1852 imply that volcanic ash deposition (volcanic ash is the major component of soils in the region) probably have profound effects on *Nothofagus* regeneration and growth in this forest. Previously, periodic disturbance by volcanism (even at large intervals) were reported to contribute to the conditions which favor the regeneration of *Nothofagus* in the mixed forests of south-central Chile (Veblen et al., 1977b, 1979b, 1980, 1981, 1992; Veblen and Ashton, 1978; Kitzberger et al., 1995). The results of this study show that disturbances such as canopy openings, ash deposition or fire can have highly variable effects across the landscape and on the dynamics of mixed *Nothofagus* forests; however, these types of disturbance facilitate the establishment and growth of *Nothofagus* species and seem to be sufficient to maintain the presence of *N. alpina* in the mixed *Nothofagus* forest studied (cf. Veblen et al., 1980, 1981, 1996). The uneven-aged trees of *N. alpina* and *N. dombeyi* in this stand result from regeneration opportunities on stand-scale that are common in mature *Nothofagus* forests at higher elevation (Veblen, 1979, 1989a,b; Rebertus and Veblen, 1993a; Rebertus et al., 1993; Veblen and Alaback, 1996). Thus, this situation is different from the forests in the Valdivian rainforest district, where *Nothofagus* spp. recruitment occurred principally after large-scale disturbances (Veblen et al., 1979b, 1981, 1996; Veblen, 1985a, 1992; Lusk, 1999).

5. Conclusions

The old-growth *N. alpina*–*N. dombeyi* forest at Conguillio National Park has been dominated by *N. alpina* since the 1500s, probably even longer. In the Andean Range (to the North of 40°S), the postglacial recolonization of treeless terrain by *Nothofagus* spp. and other species has been observed paleoecologically (Villagrán, 1991; Villagrán et al., 1995, 1998). However, the present-day high concentration of species and endemism in the study area is mainly a result of relatively stable climatic conditions that permitted maintenance of Chilean forest flora during the glacial periods in the Quaternary (Villagrán, 1994). The composition and dynamics of this forest can be explained by a complex interaction of climate, soil conditions and disturbances. It is not very likely that this forest being in steady-state conditions (until the next major disturbance), was greatly disturbed by anthropogenic factors. Neither logging nor fire scars were observed, as might be expected in even-aged forests (e.g. Kitzberger and Veblen, 1999; Veblen et al., 1999). The relatively favorable light conditions of this forest interacted with fertile soils and single treefall gaps. Continuous recruitment of *N. alpina* was found, forming an uneven-aged canopy, probably due to a relatively high frequency of disturbances. However, in *Nothofagus* forests, gap turnover times were estimated at >500 years (Veblen et al., 1981). *N. alpina* can be classified as a long-lived light-demanding pioneer species (cf. Loehle, 1988). Thus, I believe that this is an example of long-term *N. alpina* domination as a pioneer-climax species. The site is typical relative to the entire range of this species (Eskuche, 1999; Pollmann, 2001). This *N. alpina* forest represents regeneration patterns typically situated above the upper altitudinal limit of laurophyllous species. The results found for this mixed *Nothofagus* stand are similar to other studies that have reported small- and moderate-scale treefall gap dynamics in pure or nearly pure *Nothofagus* forests found at higher elevations (e.g. Veblen et al., 1996). Therefore, the pattern of pure *Nothofagus* regeneration might be representative of other regions of high altitude mixed *N. alpina*–*N. dombeyi* forests. However, at mid-elevations in the Valdivian rainforest district, where *N. alpina* occupies zonal vegetation units with laurophyllous species (Pollmann, 2001), both treefall gaps and large-scale disturbances affect *N. alpina* forest regeneration (Veblen et al., 1981). The studied stand serves as a good example of the potential for *N. alpina* and *N. dombeyi* to regenerate continuously at higher elevations in the absence of laurophyllous species and massive disturbances. In this forest, maintaining the original composition of the forest does not appear to require large-scale disturbances.

Acknowledgements

I am grateful to CONAF for permission to work in the Conguillio National Park, to R. Marín and the park rangers for their hospitality, and to F.-K. Holtmeier and two anonymous referees for their valuable comments on earlier drafts of the manuscript. I wish to thank R. Hildebrand-Vogel for introducing me to the study area. My thanks also goes to C. Lehnebach for field assistance, and to J. Huffman and R. Zamath for correcting the English. The research was supported by grants from the German Government and the German Academic Exchange Service.

References

Abrams, M.D., Copenheaver, C.A., 1999. Temporal variation in species recruitment and dendroecology of an old-growth white oak forest in the Virginia Piedmont, USA. For. Ecol. Manage. 124, 275–284.

Abrams, M.D., Orwig, D.A., 1995. Structure, radial growth dynamics and recent climatic variations of a 320-year-old *Pinus rigida* rock outcrop community. Oecologia 101, 353–360.

Abrams, M.D., Orwig, D.A., DeMeo, T.E., 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine–mixed-oak forest in the southern Appalachians, USA. J. Ecol. 83, 123–133.

Abrams, M.D., Ruffner, C.M., DeMeo, T.E., 1998. Dendroecology and species co-existence in an old-growth *Quercus–Acer–Tilia* talus slope forest in the central Appalachians, USA. For. Ecol. Manage. 106, 9–18.

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

Besoaín, E., 1985. Los suelos. In: Tosso, J. (Ed.), Suelos volcánicos de Chile. INIA, Santiago de Chile, pp. 25–107.

Brun, R., 1969. Strukturstudien im gemäßigten Regenwald Südchiles als Grundlage für Zustandserhebungen und Forstbetriebsplanung. Ph.D. Thesis. Univ. Freiburg.

Brun, R., 1975. Estructura y potencialidad de distintos tipos de bosque nativo en el Sur de Chile. Bosque 1, 6–17.

Burschel, P., Gallegos, C., Martínez, O., Moll, W., 1976. Composición y dinámica regenerativa de un bosque virgen mixto de raulí y coigüe. Bosque 1, 55–86.

Casertano, L., 1963. General characteristics of active Andean volcanos and a summary of their activities during recent centuries. Bull. Seismol. Soc. Am. 53, 1415–1433.

Clapperton, C.M., 1993. Quaternary Geology and Geomorphology of South America. Elsevier, Amsterdam.

CONAF (Ed.), 1998. Experiencia silvicultural del bosque nativo de Chile. Recopilación de antecedentes para 57 especies arbóreas y evaluación de práticas silviculturales. Salesianos S.A., Santiago de Chile.

Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. Ecology 37, 451–460.

Donoso, C., 1981. Tipos forestales de los bosques nativos de Chile. Invest. Desarrollo For. 38, 1–70.

Donoso, C., 1993. Bosques templados de Chile y Argentina. Variación, estructura y dinámica. Edit. Univers., Santiago de Chile.

Donoso, C., Lara, A. (Eds.), 1998. Silvicultura de los bosques nativos de Chile. Edit. Univers., Santiago de Chile.

Donoso, P., Donoso, C., Sandoval, V., 1993. Proposición de zonas de crecimiento de renovales de roble (*Nothofagus obliqua*) y raulí (*Nothofagus alpina*) en su rango de distribución natural. Bosque 14, 37–55.

Duncan, R.P., 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). NZ Nat. Sci. 16, 31–37.

Eskuche, U., 1999. Estudios fitosociológicos en el Norte de la Patagonia. II. Los bosques del Nothofagion dombeyi. Phytocoenologia 29, 177–252.

Finckh, M., 1996. Die Wälder des Villarrica–Nationalparks (Südchile). Lebensgemeinschaften als Grundlage für ein Schutzkonzept. Diss. Bot. 259, 1–181.

Foster, D.R., 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, southwestern New Hampshire, USA. J. Ecol. 76, 105–134.

Frank, D., Finckh, M., 1999. Laurophyllisation of deciduous *Nothofagus* forests in southern Chile. In: Klötzli, F., Walther, G.-R. (Eds.), Recent Shifts in Vegetation Boundaries of Deciduous Forests, Especially due to General Global Warming. Birkhäuser, Basel, pp. 317–331.

Freléchoux, F., Buttler, A., Schweingruber, F.H., Gobat, J.-M., 2000. Stand structure, invasion, and growth dynamics of bog pine (*Pinus uncinata* var. *rotundata*) in relation to peat cutting and drainage in the Jura Mountains, Switzerland. Can. J. For. Res. 30, 1114–1126.

Frelich, L.E., Graumlich, L.J., 1994. Age class distribution and spatial patterns in an old-growth hemlock–hardwood forest. Can. J. For. Res. 24, 1937–1947.

Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, London.

Fritts, H.C., Swetnam, T.W., 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. Adv. Ecol. Res. 19, 111–188.

Fujita, K., Sano, J., 2000. Structure and developmental process of a *Quercus mongolica* var. *grosseserrata* forest in the Fagetea crenatae region in Japan. Can. J. For. Res. 30, 1877–1885.

Gajardo, R., 1994. La vegetación natural de Chile. Clasificación y distribución geográfica. Edit. Univers., Santiago de Chile.

Gutiérrez, E., Vallejo, R., Romaña, J., Fons, J., 1991. The sub-Antarctic *Nothofagus* forests of Tierra del Fuego: distribution, structure and production. Oecol. Aquat. 10, 351–366.

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

Iseli, M., Schweingruber, F.H., 1989. Sichtbarmachen von Jahrringen für dendrochronologische Untersuchungen. Dendrochronologia 7, 145–157.

Kalela, E.K., 1941. Über die Holzarten und die durch die klimatischen Verhältnisse verursachten Holzartenwechsel in den Wäldern Ostpatagoniens. Ann. Acad. Sci. Fennicae 5A, IV 2, 1–151.

Kitzberger, T., Veblen, T.T., 1999. Fire-induced changes in northern Patagonian landscapes. Landscape Ecol. 14, 1–15.

Kitzberger, T., Veblen, T.T., Villalba, R., 1995. Tectonic influences on tree growth in northern Patagonia, Argentina: the roles of substrate stability and climatic variation. Can. J. For. Res. 25, 1684–1696.

Lamprecht, H., 1980. Zur Methodik waldkundlicher Untersuchungen in Naturwaldreservaten. Natur und Landschaft 55, 146–147.

Leuschner, H.H., 1994. Jahrringanalysen. In: Herrmann, B. (Ed.), Archäometrie. Springer, Berlin, pp. 121–135.

Loehle, C., 1988. Tree life history strategies: the role of defense. Can. J. For. Res. 18, 209–222.

Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can. J. For. Res. 19, 651–663.

Lorimer, C.G., Dahir, S.E., Singer, M.T., 1999. Frequency of partial missing rings in *Acer saccharum* in relation to canopy position and growth rate. Plant Ecol. 143, 189–202.

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

Lusk, C., 1996b. Stand dynamics of the shade-tolerant conifers *Podocarpus nubigena* and *Saxegothaea conspicua* in Chilean temperate rain forests. J. Veg. Sci. 7, 549–558.

Lusk, C., 1999. Long-lived light-demanding emergents in southern temperate forests: the case of *Weinmannia trichosperma* (Cunoniaceae) in Chile. Plant Ecol. 140, 111–115.

Marticorena, C., Quezada, M., 1985. Catálogo de la flora vascular de Chile. Gayana Bot. 42, 1–157.

Martin, C., 1923. Landeskunde von Chile. Friederichsen und Co., Hamburg.

Miller, A., 1976. The climate of Chile. In: Schwerdtfeger, W. (Ed.), Climates of Central and South America. World Surv. Climatol. 12, 113–145.

Moreno, H., Varela, J., 1985. Geología, volcanismo y sedimentos piroclásticos cuaternarios de la región Central y Sur de Chile. In: Tosso, J. (Ed.), Suelos volcánicos de Chile. INIA, Santiago de Chile, pp. 493–527.

Müller-Using, B., 1973. Untersuchungen über die Verjüngung von *Nothofagus alpina* (Poepp. et Endl.) Oerst. und ihrer wichtigsten Begleitbaumarten in der chilenischen Anden- und Küstenkordillere. Ph.D. Thesis. Univ. München.

Norton, D.A., Palmer, J.G., Ogden, J., 1987. Dendroecological studies in New Zealand. 1. An evaluation of tree age estimates based on increment cores. NZ J. Bot. 25, 373–383.

Oberdorfer, E., 1960. Pflanzensoziologische Studien in Chile. Flora Veg. Mundi 2, 1–208.

Orwig, D.A., Abrams, M.D., 1994. Land-use history (1720–1992), composition, and dynamics of oak–pine forests within the Piedmont and Coastal Plain of northern Virginia. Can. J. For. Res. 24, 1216–1225.

Peterken, G.F., 1996. Natural Woodland: Ecology and Conservation in Northern Temperate Regions. Cambridge University Press, Cambridge.

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

Pollmann, W., Vogel, A., Holtmeier, F.-K., 2000. Dendroecology and species coexistence in old-growth *Nothofagus alpina* forests in the southern Andes, Chile. Verh. Ges. Ökol. 30, 76.

Read, J., Hill, R.S., 1985. Photosynthetic responses to light of Australian and Chilean species of *Nothofagus* and their relevance to the rainforest dynamics. New Phytol. 101, 731–742.

Rebertus, A.J., Veblen, T.T., 1993a. Structure and tree-fall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego, Argentina. J. Veg. Sci. 4, 641–654.

Rebertus, A.J., Veblen, T.T., 1993b. Partial wave formation in old-growth *Nothofagus* forests on Tierra del Fuego, Argentina. Bull. Torrey Bot. Club 120, 461–470.

Rebertus, A.J., Veblen, T.T., Kitzberger, T., 1993. Gap formation and dieback in Fuego–Patagonian *Nothofagus* forests. Phytocoenologia 23, 581–599.

Rigling, A., Schweingruber, F.H., 1997. Entwicklung waldföhrenreicher Wälder im Gebiet Brienz-Wiesen (GR). Eine historisch-dendroökologische Studie. Schweiz. Z. Forstwes. 148, 173–196.

Rinn, F., 1996. TSAP©: Time Series Analysis and Presentation, Version 3.0. Reference Manual, Rinntech, Heidelberg.

Ruffner, C.M., Abrams, M.D., 1998. Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. Can. J. For. Res. 28, 347–358.

Schweingruber, F.H., 1996. Tree Rings and Environment. Dendroecology. Haupt, Bern.

Schweingruber, F.H., Aellen-Rumo, K., Weber, U., Wehrli, U., 1990a. Rhythmic growth fluctuations in forest trees of Central Europe and the Front Range in Colorado. Trees 4, 99–106.

Schweingruber, F.H., Eckstein, D., Serre-Bachet, F., Bräker, O., 1990b. Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia 8, 9–38.

Schweingruber, F.H., Wehrli, U., Aellen-Rumo, K., Aellen, M., 1991. Weiserjahre als Zeiger extremer Standortseinflüsse. Schweiz. Z. Forstwes. 142, 33–52.

Seibert, P., 1996. Farbatlas Südamerika. Landschaften und Vegetation. Ulmer, Stuttgart.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The Practice of Silviculture. Applied Forest Ecology. Wiley, New York.

Torres, H., Torres, M., 1998. Los Parques Nacionales de Chile. Una guía para el visitante. Edit. Univers., Santiago de Chile.

Uebelhör, K., 1984. Struktur und Dynamik von *Nothofagus*-Urwäldern in den Mittellagen der valdivianischen Anden Chiles. Schriftenr. Forstw. Fak. Univ. München, Bay. Forstl. Versuchs - u. Forschungsanstalt 58, 1–224.

Veblen, T.T., Ashton, D.H., Schlegel, F.M., Veblen, A.T., 1977a. Distribution and dominance of species of a mixed evergreen–deciduous *Nothofagus* forest in south-central Chile. J. Ecol. 65, 815–830.

Veblen, T.T., Ashton, D.H., Schlegel, F.M., Veblen, A.T., 1977b. Plant succession in a timberline depressed by vulcanism in south-central Chile. J. Biogeogr. 4, 275–294.

Veblen, T.T., Ashton, D.H., 1978. Catastrophic influences on the vegetation of the Valdivian Andes, Chile. Vegetatio 36, 149–167.

Veblen, T.T., 1979. Structure and dynamics of *Nothofagus* forests near timberline in south-central Chile. Ecology 60, 937–945.

Veblen, T.T., Veblen, A.T., Schlegel, F.M., 1979a. Understorey patterns in mixed evergreen–deciduous *Nothofagus* forests in Chile. J. Ecol. 67, 809–823.

Veblen, T.T., Ashton, D.H., Schlegel, F.M., 1979b. Tree regeneration strategies in a lowland *Nothofagus*-dominated forest in south-central Chile. J. Biogeogr. 6, 329–340.

Veblen, T.T., Schlegel, F.M., Escobar, B., 1980. Structure and dynamics of old-growth *Nothofagus* in the Valdivian Andes, Chile. J. Ecol. 68, 1–31.

Veblen, T.T., Donoso, C., Schlegel, F.M., Escobar, B., 1981. Forest dynamics in south-central Chile. J. Biogeogr. 8, 211–247.

Veblen, T.T., 1985a. Forest development in tree-fall gaps in the temperate rain forests in Chile. Nat. Geogr. Res. 1, 161–184.

Veblen, T.T., 1985b. Stand dynamics in Chilean *Nothofagus* forests. In: Pickett, S.T.A., White, P.S. (Eds.), The Ecology of Natural Disturbances and Patch Dynamics. Academic Press, New York, pp. 35–51.

Veblen, T.T., 1989a. *Nothofagus* regeneration in treefall gaps in northern Patagonia. Can. J. For. Res. 19, 365–371.

Veblen, T.T., 1989b. Tree regeneration responses to gaps along a transandean gradient. Ecology 70, 543–545.

Veblen, T.T., 1992. Regeneration dynamics. In: Glenn-Lewin, D.G., Peet, R.K., Veblen, T.T. (Eds.), Plant Succession. Theory and Prediction. Chapman & Hall, London, pp. 152–187.

Veblen, T.T., Kitzberger, T., Lara, A., 1992. Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. J. Veg. Sci. 3, 507–520.

Veblen, T.T., Alaback, P.B., 1996. A comparative review of forest dynamics and disturbance in the temperate rainforests of North and South America. In: Lawford, R.G., Alaback, P.B., Fuentes, E. (Eds.), High-latitude Rainforests and Associated Ecosystems of the West Coast of the Americas. Climate, Hydrology, Ecology and Conservation. Ecol. Stud. 116, 173–213.

Veblen, T.T., Donoso, C., Kitzberger, T., Rebertus, A.J., 1996. Ecology of southern Chilean and Argentinean *Nothofagus* forests. In: Veblen, T.T., Hill, R.S., Read, J. (Eds.), The Ecology and Biogeography of *Nothofagus* Forests. Yale University Press, New Haven, CT, pp. 293–353.

Veblen, T.T., Kitzberger, T., Villalba, R., Donnegan, J., 1999. Fire history in northern Patagonia: the roles of humans and climatic variation. Ecol. Monogr. 69, 47–67.

Veit, H., Garleff, K., 1995. Evolución del paisaje cuaternario y los suelos en Chile Central–Sur. In: Armesto, J.J., Villagrán, C., Arroyo, M.T.K. (Eds.), Ecología de los Bosques Nativos de Chile. Edit. Univers., Santiago de Chile, pp. 29–49.

Villagrán, C., 1991. Historia de los bosques templados del Sur de Chile durante el Tardiglacial y Postglacial. Rev. Chil. His. Nat. 64, 447–460.

Villagrán, C., 1994. Quaternary history of the Mediterranean vegetation of Chile. In: Arroyo, M.T.K., Zedler, P.H., Fox, M.D. (Eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia. Ecol. Stud. 108, 3–20.

Villagrán, C., Moreno, P., Villa, R., 1995. Antecedentes palinológicos acerca de la historia cuaternario de los bosques chilenos. In: Armesto, J.J., Villagrán, C., Arroyo, M.T.K. (Eds.), Ecología de los Bosques Nativos de Chile. Edit. Univers., Santiago de Chile, pp. 51–69.

Villagrán, C., Le-Quesne, C., Aravena, J.C., Jiménez, H., 1998. El rol de los cambios de clima del Cuanternario en la distribución actual de la vegetación de Chile Central–Sur. Bamberger Geogr. Schriften 15, 227–242.

Villalba, R., Veblen, T.T., 1997. Regional patterns of tree population age structures in northern Patagonia: climatic and disturbance influences. J. Ecol. 85, 113–124.

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

Whittaker, R.H., 1975. Communities and Ecosystems. Macmillan, New York.

Woodward, F.I., 1987. Climate and Plant Distribution. Cambridge University Press, Cambridge.