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Fire and the dynamics of *Fitzroya cupressoides* (alerce) forests of Chile's Cordillera Pelada[1]

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Abstract: Widespread mortality of *Fitzroya cupressoides* (alerce) is found throughout the Coastal Range of south-central Chile. The main explanations for tree mortality have been fire and climate change. In order to better understand the dynamics and mortality of *Fitzroya* in the Cordillera Pelada ('barren range', within the Coastal Range), we established four study plots (with varying degrees of *Fitzroya* mortality), from which we collected information on tree regeneration, age and size classes of living and dead trees, dates of fire scars from tree stumps, and radial growth rates. The abundance of seedlings and saplings in areas affected by recent, low-intensity fires indicates adequate regeneration of *Fitzroya*. Age class structures of adult *Fitzroya* trees from three of the stands show single-cohort populations, suggesting establishment after a stand-devastating disturbance. Fires from two stands were dated to years ranging between 1397 and 1943, indicating that fires have occurred repeatedly over the past 600 years. Tree growth increases immediately after fire. Based on the presence of burned snags, soil charcoal, single-cohort age structures, and numerous dated fire scars, we conclude that repeated fire is the main cause of widespread *Fitzroya* mortality in the Cordillera Pelada. Since the time of European settlement in southern Chile (*ca.*1750), fires have mainly been caused by Europeans; however, prior to that time, fires were probably caused by both lightning and native people that inhabited the area.
Keywords: Fitzroya, forest dynamics, fire, conifer regeneration, dendrochronology.

Résumé: On explique la forte mortalité de *Fitzroya cupressoides* dans la zone côtière du centre-sud du Chili par l'impact des feux ou du climat. Des données sur la régénération, la structure d'âge et de taille des individus vivants et morts, la croissance radiale des arbres, ainsi que des cicatrices de feux ont été récoltées dans quatre sites (variant selon le degré de mortalité de *Fitzroya*) pour documenter la dynamique des peuplements et identifier les facteurs de mortalité. Une abondance de plantules et de gaulis dans les sites touchés récemment par des feux de faible intensité indique une régénération adéquate de *Fitzroya*. L'analyse de la structure d'âge des arbres adultes montre la présence d'une seule cohorte de *Fitzroya* dans trois des quatre sites, suggérant un établissement après feux réussi. Dans deux sites, des feux sont survenus de manière récurrente entre 1397 et 1943. Une augmentation subite de la croissance radiale de *Fitzroya* a été observée à la suite de la forte mortalité liée à deux feux. D'après la présence d'arbres morts calcinés, de charbons dans les sols, de structures d'âge équiennes et des cicatrices de feux, des incendies récurrents sont à l'origine de la forte mortalité de *Fitzroya* dans la Cordillère de Pelada. Depuis la colonisation européenne dans le sud du Chili (vers 1750), les incendies sont surtout d'origine anthropique, alors qu'auparavant ils étaient autant d'origine naturelle qu'anthropique.
Mot-clés: Fitzroya, dynamique forestière, feu, régénération de conifères, dendrochronologie.

Introduction

Fitzroya cupressoides ([Mol.] Johnst., Cupressaceae; common name 'alerce') is a long-lived conifer endemic to the temperate rainforests of southern Chile and portions of adjacent Argentina (Figure 1). In Chile it occurs throughout the Coastal Range between Corral and Chiloé Island (latitudes 39° 50' s - 42° 35' s), and throughout the Andean Range between Cerro Puntiagudo, and Río Yelcho (41° s - 43° 30' s; Figure 1), with several stands occurring on the Argentine side of the border. Recently, several small, regenerating *Fitzroya* stands have been found in the Intermediate Depression near Puerto Montt. (Silla, 1997; Fraver *et al.*, 1999).

More than three centuries of over-exploitation, owing to the beauty and durability of *Fitzroya* wood, as well as forest conversion to agricultural use, have significantly reduced the original abundance of *Fitzroya* forests and have left extensive harvested areas (Veblen, Delmastro & Schlatter, 1976; Veblen & Ashton, 1982; Donoso *et al.*,1993). Due to this exploitation and its reduced abundance, *Fitzroya* is considered a threatened species and today is protected by law in Chile and Argentina. It is also listed under the Convention on International Trade in Endangered Species (CITES) Appendix I, forbidding its international trade (Lara & Verscheure, 1987; Lara, Donoso & Aravena, 1996). Despite this protection, illegal cutting of *Fitzroya* in Chile still occurs (Lara, Donoso & Aravena, 1996).

Fitzroya can attain a size of up to 5 m in diameter and >50 m in height, often appearing as an emergent when mixed with other species. In the Coastal Range, it occurs in pure stands or mixed with *Nothofagus nitida, Drimys winteri, Saxegothaea conspicua*, and *Podocarpus nubigena* (Donoso *et al.*, 1993). In the Andean Range it occurs with *Nothofagus betuloides* at higher elevations, and with *N. nitida, Laureliopsis philippiana* and *S. conspicua* at mid and low elevations. In extremely poorly drained areas it grows with

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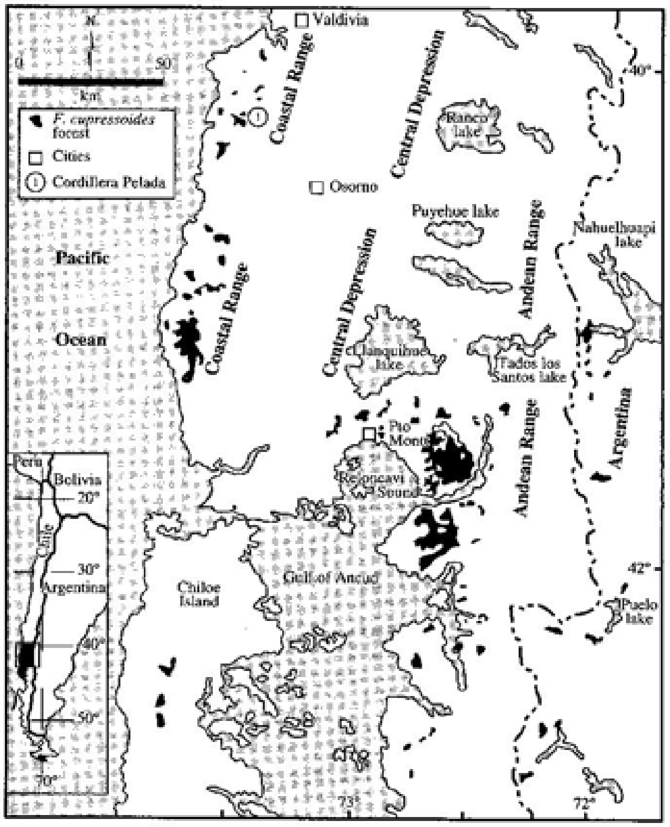

FIGURE 1. Location map of the study area in south-central Chile, indicating the distribution of *Fitzroya* forests.

Pilgerodendron uvifera in the Coastal Range and in the Andes (Lara, 1991; Donoso *et al.*, 1993). Due to the variation in topography, geology, and soils throughout its range, *Fitzroya* is found in a variety of habitats with elevations ranging from sea level to 1200 m. However, all sites are characterized by high precipitation, typically with poorly-drained, low-fertility soils where competition from other tree species is minimal (Peralta, Ibarra & Oyanedel, 1982; Veblen *et al.*, 1995).

Fitzroya can live longer than 3600 years, making it the second longest-lived species worldwide, after *Pinus longaeva* of western United States (Lara & Villalba, 1993). Dendrochronological studies using *Fitzroya* have produced a 3620 year summer temperature reconstruction, and there are currently more than 20 tree-ring chronologies over 1000 years in length (Villalba, 1990; Lara & Villalba, 1993; 1994; Villalba *et al.*, 1996).

Fitzroya is a shade-intolerant species that regenerates by seed as well as vegetatively; however seed production is sporadic, with a high percentage of trees producing non-viable seeds (Donoso, 1993; Donoso, Cortés & Escobar, 1993). In Chile, *Fitzroya* regeneration modes (*sensu* Veblen, 1992) vary between the Andean and the Coastal Ranges. In the Andes, *Fitzroya* regeneration under closed-canopy, undisturbed forests is essentially absent, and the main regeneration mode is catastrophic, following large-scale disturbances such as landslides and volcanic ash deposition (Veblen, Delmastro & Schlatter, 1976; Lara, 1991; Donoso *et al.*, 1993). In addition to this catastrophic regeneration mode, *Fitzroya* also regenerates at a slow, sporadic rate in open-canopy, undisturbed forests located over 800 m of elevation (Lara, 1991). Some authors have reported regeneration in fine-scale tree-fall gaps, although there is no agreement about its significance for the persistence of the species (Donoso *et al.*, 1993; Veblen *et al.*, 1995). In the Coastal Range *Fitzroya* regenerates following low-intensity fires and in some cases logging, provided that parent trees remain and intensive cattle grazing does not occur (Veblen & Ashton, 1982; Cortés, 1990; Parker & Donoso, 1993). Conversely, in the Andes *Fitzroya* regeneration does not occur after selective logging, clearcuts, or human-set fires (Veblen, Delmastro & Schlatter, 1976; Lara, 1991; Donoso *et al.*, 1993).

One of the most striking features of *Fitzroya* forests in the Coastal Range is the widespread mortality. Here, especially on gentle slopes at higher elevations, the landscape is dominated by stands of barkless, semi-bleached *Fitzroya* snags mixed with varying proportions of living trees. The local name of this range which lies between 39° 50' s and 41° 30' s is Cordillera Pelada meaning 'barren range', referring to this landscape pattern. The widespread mortality of *Fitzroya* in this area was reported at least since the 1860s by Philippi (1865). After a botanical reconnaissance of the Cordillera Pelada, Philippi described the extensive dead *Fitzroya* stands, and although he did not report evidence of fire, he speculated about an old extensive fire as a possible cause of stand mortality (Philippi, 1865).

Palynological studies (Heusser, 1966; 1982) indicate that *Fitzroya* has decreased in abundance since 3000 BP as a result of a regional decline in precipitation. Heusser (1982) suggested that the death of the *Fitzroya* stands in the Cordillera Pelada may have resulted from climate change, although he acknowledged the occurrence of fire in the area. Heusser's idea is consistent with the hypothesis proposed by Schmithüsen (1960) that *Fitzroya* is a climatic relict, which is being replaced by broad-leaved species.

Other studies from Cordillera Pelada present a different explanation for *Fitzroya* mortality in Cordillera Pelada. Veblen & Ashton (1982) mainly attributed the widespread *Fitzroya* mortality to fire, pointing to the presence of fire-scarred trees and burned stumps. Similarly, a study of disturbance history and vegetation along a soil-fertility gradient in the Cordillera Pelada indicates that fire is the main disturbance type in low-fertility sites occupied by *Fitzroya* forests, whereas blowdowns dominate on more fertile sites where *Nothofagus nitida* forests occur (Lusk, 1996). Although this study does not provide information on fire dates, ages of post-fire stands indicate that fires were an important disturbance even before the European settlement in southern Chile (*i.e.*, before *ca.* 1750, Lusk, 1996).

Neither fire history from tree-rings nor their specific influence on forest dynamics have been studied in southern Chile. Conversely, the adjacent northern Patagonia region of Argentina has provided fire chronologies from *Austrocedrus chilensis* tree-rings since AD 1439, demonstrating climatic influences on fire frequency, especially related to drought episodes, in fires set by lightning and human native populations prior to the 1890s and European settlers thereafter (Kitzberger, Veblen & Villalba, 1997; Kitzberger & Veblen, 1997). To our knowledge, the present study is the first published work from southern Chile that provides fire-history data obtained from tree-rings and specifically addresses the influence of fire on forest stand dynamics.

The purpose of this study was to determine the role of fire in the dynamics and mortality of *Fitzroya* stands in the Cordillera Pelada. If fire played an important role in the dynamics of *Fitzroya*, then: *i)* stand structure would reflect single, relatively even-aged cohorts that originated after fire, *ii) Fitzroya* seedlings and saplings would be abundant in stands opened by recent fires, indicating successful recruitment, and *iii)* tree growth patterns would show marked periods of rapid growth releases following dated fires.

Study area

The Cordillera Pelada extends roughly between the Valdivia and the Río Bueno rivers, reaching its highest elevation at El Mirador (1048 m), at *ca.* 40° 10' s. The Cordillera consists of gentle slopes and flat mountain plateaus, with metamorphic bedrock of Paleozoic to Precrambrian age (Villagrán *et al.*, 1993). Soils vary considerably in the upper elevations of the Cordillera (*i.e.*, above 800 m), influencing important variation in vegetation patterns (Lusk, 1996). Higher fertility sites are represented by well-drained brown loams, and are covered by mixed valdivian forests dominated by *Nothofagus nitida, Laureliopsis philippiana, Saxegothaea conspicua,* and *Weinmannia trichosperma.* Poor sites have thin, acidic, sandy, and poorly drained soils with varying degrees of gley formation, and are typically covered by *Fitzroya cupressoides*, mixed with varying proportions of *Nothofagus nitida, N. betuloides, S. conspicua, W. trichosperma,* and *Drimys winteri*. In the most poorly drained sites, *Fitzroya* occurs with *Pilgerodendron uvifera* and *N. betuloides*. *Fitzroya* can attain a height of 30 to 40 m at lower elevations or in deeper soils in the Cordillera, but dwarfs dramatically towards the summit of El Mirador where it grows in very thin and infertile soils in almost pure stands with height < 5 meters.

In the Cordillera Pelada, *Fitzroya* stands are often open (crown cover < 50%), with a dense shrub cover, consisting principally of bamboo, *Chusquea nigricans*, along with *Desfontainea spinosa, Berberis serrato-dentata*, and other species (Ramírez & Riveros, 1975; Heusser, 1982). The understory is also characterized by a dense layer of epiphytes dominated by *Philesia magellanica*, as well as a dense mat of bryophytes such as *Sphagnum spp.* and *Rhacomitrium lanuginosum* (Veblen & Ashton, 1982). This dense understory becomes very dry during episodic summer droughts. The Cordillera Pelada's climate is classified as cold-temperate maritime, with very high annual precipitation. Average July and January temperatures are 8°C and 16°C, respectively (Almeyda & Sáez, 1958). Annual precipitation exceeds 4000 mm, with 40% occurring during the winter months (Heusser, 1982). Snowfall is common between June and August.

The *Fitzroya* stands we sampled are located in Monumento Natural Alerce Costero and in adjacent private land of the Cordillera Pelada. We selected four stands that represent different degrees of fire disturbance: stands A (most recently disturbed) through D (disturbance-free for a long period). The stands are located on fairly level terrain (slopes ranging from 3° to 16°) and at similar elevations (from 800 to 990 m), near the local landmark known as Piedra del Indio, and directly west along the road to El Mirador. Sites are separated by a distance < 5 km. Due to probable differences in soil properties (nutrients and drainage) that affect potential basal areas and canopy structure, the sites cannot be regarded as a chronosequence. The degree of dominance of *Fitzroya* in the various stands range from almost pure to mixed stands with species such as *Nothofagus betuloides, Nothofagus nitida, Drimys winteri,* and *Pilgerodendron uvifera*. Canopy cover varies among the sampled stands. Stand A has an open canopy, whereas stands B and D are semi-dense and stand C is dense.

Material and methods

In 1993 we established one study plot in each of the four stands. Plots ranged in size from 200 to 1000 m^2, depending on the stage of stand development and tree density. We collected information on seedling frequency and sapling density, age and size structures of living and dead trees, dates of fire scars from stumps, and radial growth rates of living trees.

In each plot we measured tree diameters of living and dead trees > 5 cm diameter at breast height (dbh). From these same trees, we extracted one or two increment cores at *ca.* 30 cm height above ground for age determination and construction of tree-ring width chronologies. We recorded the number of saplings (individuals of tree species < 5 cm dbh and ≥ 2 m in height) per species in the entire plots and we determined frequency of seedlings (individuals of tree species < 2 m in height) based on 20 4 m^2 subplots (2 × 2 m) arranged at 5 m intervals along the inside borders of plots, or in belt transects in the case of 200 m^2 plots.

To determine tree ages, we used standard tree-ring methods of Stokes & Smiley (1968). Since most tree cores did not reach the pith, the number of rings to center was estimated by Duncan's (1989) method. The main limitation of this method is that it assumes that rings form concentric circles around the pith, and that ring width is constant in the missing part of the sample (Villalba & Veblen, 1997; Kitzberger, Veblen & Villalba, in press). Most of the estimated error of the number of rings-to-center is due to differences in growth rate between the missing radius and the measured part of the core (Duncan, 1989). From our tests on *Fitzroya* cross-sections and given that we selected 50 year age classes, we accepted a maximum estimate of 25 rings-to-center using Duncan's (1989) method. Samples that presented a higher number of estimated rings-to-center were treated as minimum ages. Cores with rotten centers, in which the intact portion represented at least 75% of the radius length, were also included under the minimum ages; samples with a smaller percentage of intact core were discarded. All ages for the age structure analysis are expressed at coring height (30 cm from the ground). No data were collected in the Cordillera Pelada to determine the number of years required for a *Fitzroya* seedling to reach coring height. Available data from the Andes, where radial growth of *Fitzroya* is much slower than in the Cordillera Pelada, indicate that it takes 16 to 26 years for a seedling to reach coring height (Lara, 1991). Therefore, age estimates from samples at coring height in the Cordillera Pelada probably underestimate the actual ages (*i.e.*, age since germination) by 10 to 20 years.

We used standard dendrochronological methods to produce tree-ring width chronologies for each site in order to investigate growth patterns as well as the occurrence of growth releases and suppressions and their relation to fire and *Fitzroya* regeneration events. These methods include cross-dating in order to identify the exact calendar year in which each ring was formed. (Stokes & Smiley, 1968; Fritts, 1976). Visual cross-dating and possible measurement errors were checked and improved using the COFECHA program (Holmes, 1983). Cross-dated tree-ring series were standardized, and an average tree-growth series for each site was developed by converting ring widths to a non-dimensional index. Standardization consisted of transforming each tree-ring width series from individual trees by dividing the measured values from individual trees by the value of a horizontal line fit through them. This procedure does not remove a tree's biological growth trend (decreasing tree-ring width attributable to tree age); it was chosen because it preserves most of the low-frequency ring-width variation and is particularly useful in identifying periods of release such as those related to canopy disturbance (Veblen *et al.*, 1991). Standardization, as well as the construction of tree-ring chronologies, was carried out using the ARSTAN program (Cook & Holmes, 1984).

The various sampled stands and neighboring areas were searched for stumps with fire scars, following methods described by Dietrich & Swetnam (1984). The fact that *Fitzroya* is a protected species precluded the collection of samples from living trees with fire scars. The collection of cross sections from stumps with fire scars was restricted to stand B and Piedra del Indio, a burned and logged area located about 800 m from stand C, where scarred stumps were available. The search area in stand B was *ca.* 0.3 ha, and in Piedra del Indio, *ca.* 0.5 ha, thereby emphasizing fire history at a stand scale. The year in which each fire scar was formed as well as the inner and outermost rings on stumps were determined by measuring ring widths on the cross-sections and using COFECHA (Holmes, 1983) which statistically compares the measured ring-width series with a master tree-ring chronology developed for El Mirador (Neira, 1995), following the methods described by Kitzberger & Veblen (1997), and Kitzberger, Veblen & Villalba (in press). We followed Schulman's (1956) convention and assigned dates of annual rings to the year in which ring formation begins. Therefore for *Fitzroya*, the calendar year is that of October through December. A fire scar in earlywood or latewood of a particular year would indicate fire occurrence between October of that year and March of the following year. Fire scars in the dormant season were not found. Fire records kept by CONAF (1997) since 1978, indicate that fires occur mainly between December and March of the following year. On several samples, fires could not be dated to a particular year, since the rings around the scar were rotten. In these cases, fire dates were treated as approximations, and were adjusted to match exactly-dated fire years when they fell within five years from them. Fire dates obtained in this way were used to produce a fire chronology for stands B and Piedra del Indio following the methods described by Dietrich (1980).

Results

AGE AND SIZE STRUCTURES

Stand structure varied significantly among stands in terms of age range, dominance of *Fitzroya*, and prevalence of dead *Fitzroya*. Age of oldest trees on each site ranged from 59 to 959 years (Table I), considering only total age from cores that reached the pith or cores with ≤ 25 years-to-center estimated according to Duncan's (1989) method. In stands A, B and C, *Fitzroya* was the dominant tree species, with a

TABLE I. Age and dbh ranges, densities, basal areas, percentage of fire-scarred trees, and other structural features of the four sampled stands. Age range refers to total age with pith and total age estimated by Duncan's (1989) method

Stand	Species	Live trees DBH range (cm)	Age range (years)	Live density (No./ha)	Basal area (m^2/ha)	Dead density (No./ha)	Basal area (m^2/ha)	Percentage of dead basal area over total (%)	Percentage of living trees with fire scars (%)	Canopy density
A	*Fitzroya cupressoides*	(5-21)	(59-86)	2250	25.2	850	109.7	81	5	Open
	Drimys winteri	(6-20)	(47-70)	350	4.5	50	0.7	13		
	TOTAL			2600	29.7	900	110.4			
B	*Fitzroya cupressoides*	(13-46)	(117-257)	763	47.7	650	39.9	45	84	Semi-dense
	Nothofagus betuloides	(6-36)	(21-103)	25	1.3					
	Drimys winteri	(8)	(52)	25	0.2					
	Weinmannia trichosperma	(5-6)	(31-50)	50	0.1					
	TOTAL			863	49.3	650	39.9			
C	*Fitzroya cupressoides*	(10-55)	(130-296)	2550	95.9	1400	32	25	0	Dense
	Nothofagus betuloides	(36-48)	(223-273)	150	19.3					
	Nothofagus nitida	(10-11)	(95-117)	100	0.9					
	Saxegothaea conspicua	(6-7)	(82-194)	100	0.4					
	TOTAL			2900	116.3	1400	32			
D	*Fitzroya cupressoides*	(5-65)	(190-959)	310	22.8	90	18.8	45	3	Semi-dense
	Nothofagus betuloides	(8-42)	(59-186)	430	15.6	50	1.6	9		
	Drimys winteri	(5-19)	(50-194)	130	1.8					
	Pilgerodendron uvifera	(6-17)	(138-755*)	230	4.8					
	TOTAL			1100	45	140	20.4			

* : Minimum age

relative basal area of 85% (the three stands pooled); however, in stand D it shared dominance with other species, where it represented 51% of the live basal area (Table I). The abundance of dead *Fitzroya* ranged between 25 and 81% (dead basal area expressed as a percent of the total basal area; Table I). The stands also varied greatly in the percentage of living *Fitzroya* trees showing fire scars (from 0 to 84%).

Age and size class distributions for *Fitzroya* in each stand are shown in Figure 2. Most total ages in every stand required estimates of rings-to-center reflecting the difficulties in reaching the pith with an increment borer. Stand A was the youngest of the four stands. There, *Fitzroya* regenerated after a stand-devastating fire as indicated by the presence of a dead *Fitzroya* cohort with dbh-classes ranging from 35 to 70 cm (Figure 2) and the presence of charred dead standing and fallen trees. The age-class distribution for stand A indicated a young single-cohort, even-aged population of *Fitzroya* (with total age between 59 and 86 years old and dbh from 5 to 21 cm) that regenerated synchronously following fire (Figure 2, Table I). A relatively wide size class distribution for *Fitzroya* reflects variation in growth rates within a single cohort (Figure 2). The young cohort replaced a former *Fitzroya* population represented today by the dead trees. The amount of dead basal area (expressed as a percentage of the total) is 81%.

Stand B was a young post-fire stand as indicated by the presence of charred snags, fallen logs and large dead trees. It had a left-skewed, bell-shaped age-class distribution, indicating an even-aged stand with total age ranging from 117 to 257 years and dbh from 13 to 46 cm (Figure 2, Table I). The size distribution was also bell-shaped, reinforcing its single-cohort character (Figure 2). In this stand, 84% of the living trees had one or two fire scars, reflecting *Fitzroya's* ability to survive low-intensity fires. Fire dates of 1876 and 1943 were determined from cut stumps (Figure 3).The percentage of dead basal area was 45%, and the presence of abundant dead trees in the small size classes suggests that these trees belonged to the same cohort as the living trees and that they were killed by 1876 and/or 1943 fires (Figure 2, Table I).

Stand C was also a single cohort, even-aged stand with age and size class distributions similar to stand B: age ranged from 130 to 296 years and dbh from 10 to 55 cm (Figure 2, Table I). The presence of large dead trees in stand C, together with its age class distribution, indicate that it rapidly became established after a stand devastating disturbance, perhaps fire. The lack of fire scars on living trees reflects the absence of recent fire. Stand C was a dense, closed-canopy stand with the highest living basal area among all the stands (116.5 m^2/ha) and the lowest percentage of dead basal area (25%, Table I).

Stand D was an old-growth mixed-species stand where *Fitzroya* shares dominance with *Nothofagus betuloides*, *Pilgerodendron uvifera*, and *Drimys winteri* (Figures 2 and 4).

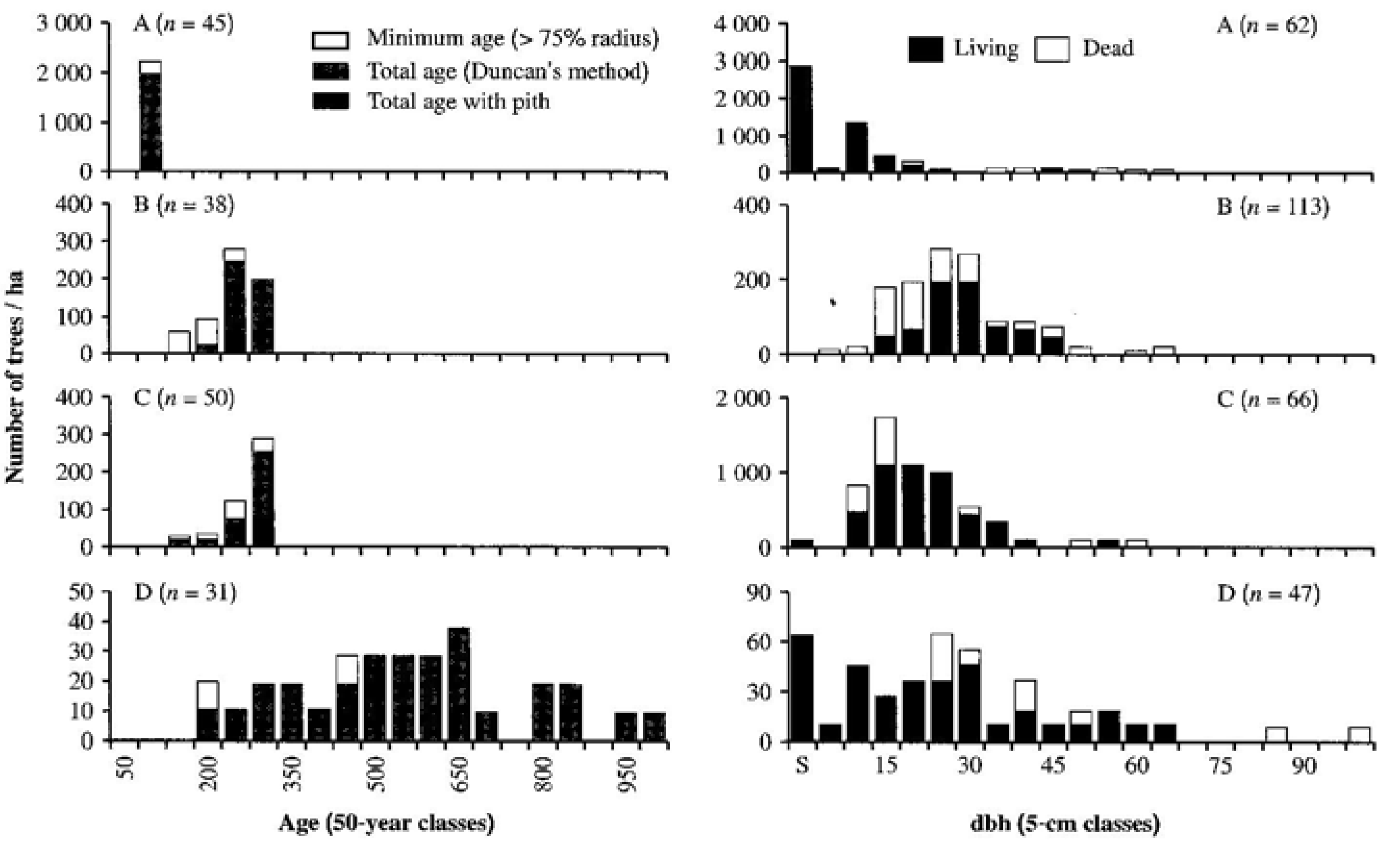

FIGURE 2. Age- and size-class distribution of *Fitzroya* in the four sampled stands (A-D).

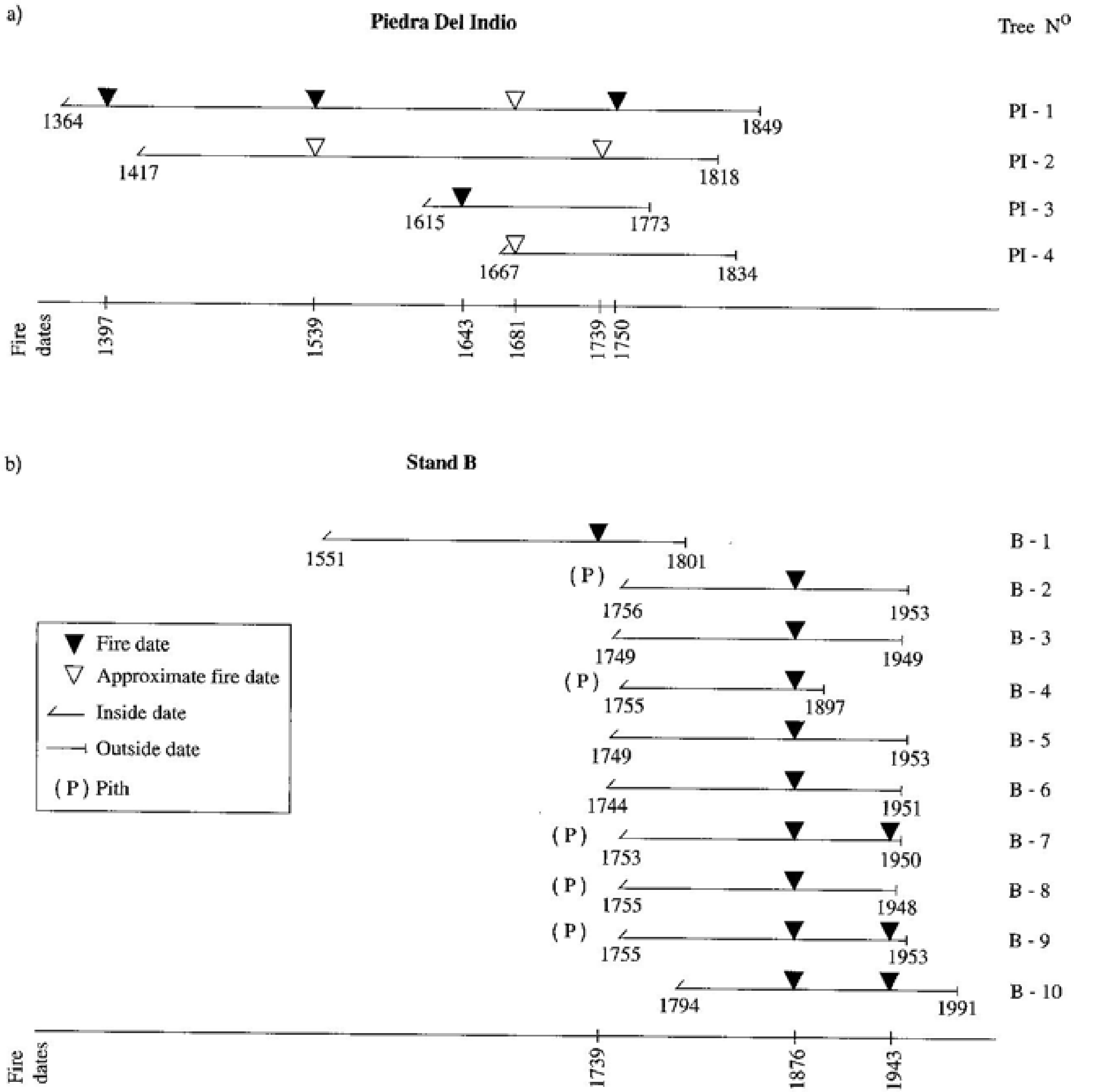

FIGURE 3. Fire chronologies for (a) stand Piedra del Indio and (b) stand B showing for each tree the length of the series and the occurrence of fire.

The presence of *Pilgerodendron* suggests poorer drainage than on the other study sites. The age class distribution for *Fitzroya* and *Pilgerodendron* showed wide age ranges (190 to 959 and 138 to 755 years, respectively, Figures 2 and 4, Table I) probably indicating slow or sporadic regeneration in a poorly-drained site. *Nothofagus betuloides* and *Drimys winteri* have younger and narrower age class distributions compared to *Fitzroya* and *Pilgerodendron* (Figure 4). Fire scars were present in 3% of the living trees, indicating that the stand has been little affected by fire. Nevertheless, since some trees were over 900 years in age, earlier fire scars might have been fully covered by tree growth. Although stand origin is not clear, the presence of *Fitzroya* snags with diameter much larger than living trees, may indicate a post-fire origin. This stand had a percentage of dead basal area of 45%, and a relatively low tree density for *Fitzroya* compared to the total (Table I).

SEEDLING AND SAPLING ABUNDANCE

Fitzroya seedling frequencies and sapling densities varied significantly among the stands (Table II). *Fitzroya* saplings were abundant in stand A (2950 individuals/ha), under the stand's open canopy, which is due to its young age. Other tree species have low sapling densities and low seedling frequencies (Table II). Although age was not determined for *Fitzroya* saplings, it is likely that many of them

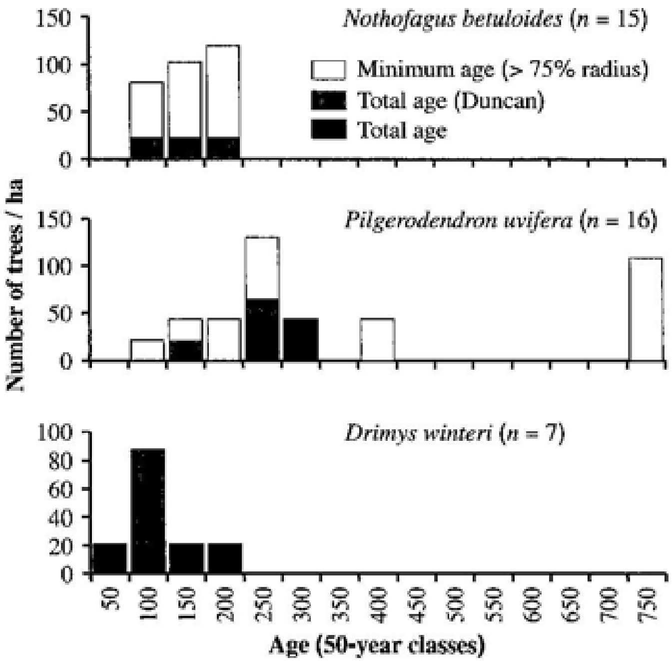

FIGURE 4. Age-class distribution for *Drimys winteri, Pilgerodendron uviferum*, and *Nothofagus betuloides* in stand D.

are suppressed individuals that belong to the main post-fire cohort shown in Figure 2. In addition, stand A had the highest frequency of *Fitzroya* seedlings (90%) among all the studied stands, suggesting that tree establishment is still taking place. Although the origin of seedling-sized *Fitzroya* (vegetative reproduction or seed) was not determined, several individuals were from root suckers as also noted by Veblen & Ashton (1982) in the Cordillera Pelada. No *Fitzroya* saplings were present in stand B, although seedling frequency was 35% (Table II). Conversely, we found abundant regeneration of other tree species, such as *Weinmannia trichosperma* with 550 saplings/ha and several individuals reaching the size of small trees < 6 cm dbh (Tables I and II).

TABLE II. Seedling frequency (from 20 subplots of 4m^2 quadrats) and sapling density for the sampled stands

Species	Seedling percentage frequency * Site				Sapling density (No./ha) Site			
	A	B	C	D	A	B	C	D
Fitzroya cupressoides	90	35			2950		50	175
Nothofagus betuloides		15	45		50	125		425
Nothofagus nitida	10		5					50
Drimys winteri	20	40	50			63		175
Embothrium coccineum	5	25				63		50
Lomatia ferruginea	15	5				150		25
Ovidia pillo-pillo		10				38		
Pilgerodendron uvifera								25
Pododcarpus nubigena			70					275
Pseudopanax laetevirens		35	25					
Saxegothaea conspicua			25					400
Tepualia stipularis							13	
Weinmannia trichosperma	5	40					550	

* See text

In stand C, only one *Fitzroya* sapling was present (which translates to 50 individuals/ha), and no seedlings were present. This lack of recruitment can be explained by the dense canopy and a living basal area twice that of stands B and D (Table I). Shade-tolerant *Saxegothaea conspicua* shows better recruitment, with a sapling density of 400 individuals/ha and a seedling frequency of 25%. The low abundance of *Fitzroya* saplings (175 individuals/ha) and the absence of seedlings in stand D, indicate a low rate of *Fitzroya* recruitment in this semi-dense stand (Table II). Sapling densities indicate that other more shade-tolerant species such as *Nothofagus betuloides, Podocarpus nubigena*, and *Drimys winteri* are also regenerating in this mixed stand.

FIRE HISTORY

With the fire dates determined from fire-scarred *Fitzroya* stumps, we produced a fire chronology for stand B and for Piedra del Indio (Figure 3). These chronologies show that some fires could be dated exactly, whereas others were dated only approximately, since the rings around the scar were rotten. We dated a total of 21 fire scars. Our results indicate that *Fitzroya* can survive low-intensity fires, forming up to four fire scars on the same tree (tree PI-1, Figure 3). The oldest dated fire occurred in 1397 (Piedra del Indio) and the most recent in 1943 (stand B; Figure 3). The lack of stumps where fire scars could be seen in stands A, C, and D prevented fire dating.

In stand B, the oldest fire scar was dated to 1739, from a tree that formed part of a previous cohort. In this stand, the trees that formed the main cohort became established between the years 1744 and 1756 (based on innermost rings and pith dates at ground level) (Figure 3). These dates indicate that most *Fitzroya* trees became established between 5 and 17 years after the 1739 fire. The relationship between fire and *Fitzroya* establishment in Piedra del Indio could not be determined because the area was completely logged and no age structure data were collected.

In addition, growth patterns in stand B since 1795 are clearly related to the occurrence of fire (Figure 5). The two sharp and rapid growth releases on the trees that survived both fires, one beginning in 1878 and the other in 1945, follow the fires dated in 1876 and 1943 and are probably the result of reduced competition among the survivors, following the fire-caused mortality of many trees. Growth patterns from the remaining three stands do not show increases in growth that may be associated with fires, and are therefore not shown.

Discussion

The presence of trees with fire scars in stands A, B, and D (with 84% of the living trees showing fire scars in stand B), as well as the abundance of charred trees and charcoal on the forest floor suggests that fire has been a major disturbance in the *Fitzroya* forests in the Cordillera Pelada. Fire has occurred repeatedly in the area, with the earliest dated fire occurring in 1397 and the most recent in 1943. It should be noted that due to the declining number of fire-scarred stumps of trees that lived prior to *ca.* 1750, the number of

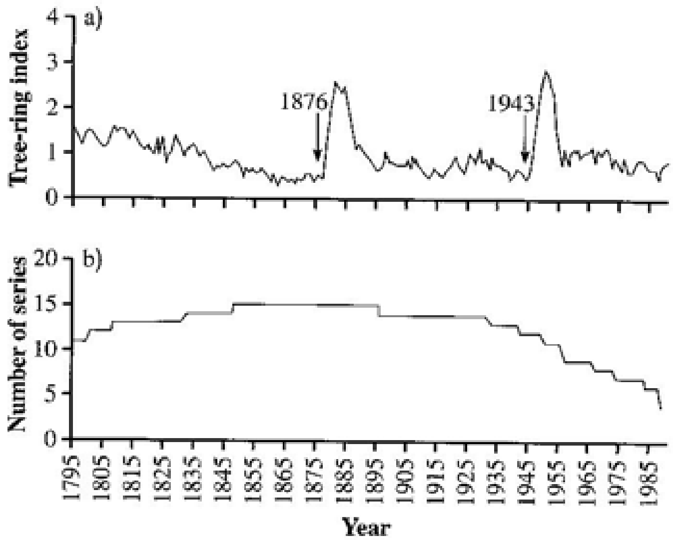

FIGURE 5. (a) Tree-ring chronology for stand B using a horizontal standardization. Tree-ring indices provide a non-dimensional value that represents growth patterns. Mean series intercorrelation from COFECHA (Holmes, 1983) is 0.457. Arrows indicate the occurrence of fires. (b) Number of radii in the tree-ring chronology.

fires occurring during this period is probably underestimated. Similarly, since only one stump covers the post-1953 period, and all samples came from dead trees, fires occurring after this date would not have been recorded. Reliable fire records from the area that could provide information for recent decades are not available. The recurrence of fire in the area and its potential role in forest dynamics is reflected by fire intervals of 67 and 137 years in stand B, and 104, 107, and 147 years for Piedra del Indio. These intervals take into account only those fires that could be precisely dated (Figure 3), and given the small number of samples, should be considered only as rough estimates.

Age class structures for stands A, B, and C indicate single-cohort, even-aged stands that originated after stand-devastating fires. This post-fire origin is especially clear in stand B, where the pith dates of the trees that were part of the main cohort indicate that they became established after the 1739 fire recorded on one tree (Figure 3). The even-aged character of the stands A, B, and C, (which are clearly dominated by a single cohort of *Fitzroya*, with a maximum age of 296 years) contrasts with the uneven-aged structure of stand D, a mixed-species, old-growth stand where *Fitzroya* represents 51% of the living basal area (sharing its dominance with *N. betuloides*) and has a maximum age of 959 years. In this stand the uneven-aged structure of *Fitzroya* and *Pilgerodendron* is probably due to slow or sporadic regeneration under a semi-open canopy and reduced competition in a poorly-drained site.

In general, *Fitzroya* seedling frequencies and sapling densities indicate that recruitment takes place in open stands that have been more recently disturbed by stand-devastating fires (stand A for example). Although there is a trend toward reduced *Fitzroya* recruitment in older stands, as the canopy closes and competition by other species increases, there are some variations to this pattern, and the interpretations are limited by the fact that no seedling or sapling ages were determined. In particular, under the semi-open canopy of stand B, which was affected by fires in 1739, 1876, and 1943, we would have expected a higher density of *Fitzroya* saplings and young trees established following the last two fires. It is not clear why they are not present at this site, where other relatively shade-intolerant species such as *Weinmannia trichosperma*, *Lomatia ferruginea*, and *N. betuloides* are present as saplings. The presence of *Fitzroya* saplings in the old-growth stand D might be related to poor drainage and reduced competition under a semi-open canopy.

As predicted, we found growth releases that immediately followed dated fires, indicating that individual *Fitzroya* trees can survive fire, taking advantage of the reduced competition and increase in resources that typically follow fires. Veblen & Ashton (1982) also report that *Fitzroya* is capable of surviving low-intensity fires, yet seems unable to survive high-intensity fires.

In the Chilean Andes, *Fitzroya* establishment occurs after landslides, volcanic ash deposition, and lava flows; however, adequate regeneration does not occur after human-set fires or timber exploitation (Veblen, Delmastro & Schlatter, 1976; Lara, 1991; Veblen *et al.*, 1995). The results from this study and those of Veblen & Ashton (1982) indicate that *Fitzroya* regeneration in Cordillera Pelada can follow stand-devastating fire, provided that the fire is not high-intensity, and that there is a nearby colonizing source that provides either seeds or sucker sprouts. Thus, *Fitzroya* forests of the Cordillera Pelada, and probably of other areas in the Coastal Range differ from those of the Chilean Andes in both their disturbance regime and their ability to regenerate following fire. Differences in *Fitzroya* forest responses to fire between both areas suggest reduced competition from other species under lower soil nutrient availability of the Cordillera Pelada compared to the Chilean Andes, but this interpretation needs to be investigated.

The dated fires reported here indicate that some fires occurred prior to the European settlement of the Chilean Lake District which began *ca.* 1750, despite the fact that the city of Valdivia (80 km from our study site) was funded in 1547. It was not until *ca.* 1850 that extensive settlement took place in the Central Depression, which led to massive burning and exploitation of alerce forests (Elizalde, 1970; Wilhelm, 1968). In the pre-European settlement period (*i.e.*, prior to *ca.* 1750), fires may have been started both by the native Huilliches, who traveled through the Cordillera Pelada, as well as by lightning that occasionally occurs during spring and summer storms. Both sources of ignition have also been mentioned for this period in Cordillera Pelada by Lusk (1996) who points out the difficulties in distinguishing them. The occurrence of extensive fires in the wet climate that characterizes *Fitzroya* forests of the Cordillera Pelada can be explained by the Mediterranean influence that brings summer drought as far south as latitude 42° s in Chile, and by the flammability of *Fitzroya* (Lusk, 1996). Moreover, the dense understory dominated by *Chusquea nigricans* and by mats of epiphytes and bryophytes becomes very dry and prone to fire during episodic summer drought.

Evidence from historical documents of fire ignition by native American hunters in northern Patagonia, Argentina, during pre-European Settlement (*i.e.*, prior to *ca.* 1890-1900) has been presented by various authors (Veblen & Lorenz, 1988; Veblen & Markgraf, 1988; Markgraf & Anderson, 1994). Studies based on fire chronologies developed from *Austrocedrus chilensis* in northern Patagonia, Argentina, beginning in 1439 AD, demonstrated that changes in fire regimes are the result of both climate variability and changes in human activities (Kitzberger & Veblen, 1997; Kitzberger, Veblen & Villalba, 1997).

Our results show that repeated fires have played a major role in the dynamics of *Fitzroya* forests in Cordillera Pelada, at least during the last 600 years, and that fire is the main cause for widespread *Fitzroya* mortality in this area. These results corroborate those of Veblen & Ashton (1982) who implicate intense fire as the cause of *Fitzroya* mortality in this area, and those of Lusk (1996) who reports that fire has been the main disturbance that has shaped the present structure of *Fitzroya* stands in Cordillera Pelada. These findings do not seem consistent with Heusser's (1982) claims that *Fitzroya* mortality and decline are mainly due to a reduction in precipitation since 3000 BP. Nevertheless, further research is needed to better understand the influence of climatic fluctuations on the fire regimes and on the dynamics of *Fitzroya* forests throughout its range.

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Literature cited

Almeyda, A. E. & S. F. Sáez, 1958. Recopilación de datos climáticos de Chile y mapas sinópticos respectivos. Ministerio de Agricultura, Santiago.

Cook, E. R. & R. L. Holmes, 1984. Users manual for program ARSTAN. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona.

CONAF (Corporación Nacional Forestal), 1997. Información estadística histórica de ocurrencia y daño por incendios forestales: Período 1978 - 1997. Puerto Montt.

Cortés, M. A., 1990. Estructura y dinámica de los bosques de alerce (*Fitzroya cupressoides* [Mol.] Johnston) en la Cordillera de la Costa de la Provincia de Valdivia. Thesis, Ciencias Forestales, Universidad Austral de Chile, Valdivia.

Dietrich, J. H., 1980. The composite fire interval: A tool for more accurate interpretation of fire history. Pages 8-14 *in* M. A. Stokes & J. H. Dietrich, (eds.). Proceedings of the Fire History Workshop, October 20-24, 1989, Tucson, Arizona. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Dietrich, J. H. & T. W. Swetnam, 1984. Dendrochronology of a fire-scarred ponderosa pine. Forest Science, 30: 238-247.

Donoso, C., 1993. Producción de semillas y hojarasca de las especies del tipo forestal alerce (*Fitzroya cupressoides*) de la Cordillera de la Costa de Valdivia, Chile. Revista Chilena de Historia Natural, 66: 53-64.

Donoso, C., V. Sandoval, R. Grez & J. Rodríguez, 1993. Dynamics of *Fitzroya cupressoides* forests in southern Chile. Journal of Vegetation Science, 4: 303-312.

Donoso, C., M. Cortés & B. Escobar, 1993. Efecto de árbol semillero y la época de cosecha de semillas en la capacidad germinativa en vivero de *Fitzroya cupressoides*. Bosque, 14: 63-71.

Duncan, R. P., 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). New Zealand Natural Sciences, 16: 31-37.

Elizalde, R., 1970. La sobrevivencia de Chile. Ministerio de Agricultura, Servicio Agrícola y Ganadero, Santiago.

Fraver, S., M. E. González, F. Silla, A. Lara & M. Gardner, 1999. Composition and structure of remnant *Fitzroya cupressoides* forests of Chile's Central Depression. Journal of the Torrey Botanical Society, 126: 49-57.

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

Heusser, C. J., 1966. Late-Pleistocene pollen diagrams from the province of Llanquihue, southern Chile. Proceedings of the American Philosophical Society, 110: 269-305.

Heusser, C. J., 1982. Palynology of cushion bogs of the Cordillera Pelada, Province of Valdivia, Chile. Quaternary Research, 7: 71-92.

Holmes, R. L., 1983. Computer-assisted quality control in tree-ring dating and measurements. Tree-Ring Bulletin, 44: 69-75.

Kitzberger, T. & T. T. Veblen., 1997. Influences of humans and ENSO on fire history of *Austrocedrus chilensis* woodlands in northern Patagonia, Argentina. Écoscience, 4: 508-520.

Kitzberger, T., T. T. 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.

Kitzberger, T., T. T. Veblen & R. Villalba, (in press). Métodos dendroecológicos y sus aplicaciones en estudios de dinámica de bosques templados de Sudamérica. *in* F. Roig (ed.). Dendrocronología en Sudamérica, Mendoza, Argentina.

Lara, A., 1991. The dynamics and disturbance regimes of *Fitzroya cupressoides* forests in the south-central Andes of Chile. Ph.D. Thesis, Department of Geography, University of Colorado, Boulder, Colorado.

Lara, A. & H. Verscheure, 1987. An urgent plan of action for the conservation of alerce (*Fitzroya cupressoides*). Final Report, Project 6045. World Wildlife Fund-US/Comité Pro Defensa de la Flora y Fauna (CODEFF), Santiago.

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. & R. Villalba, 1994. Potencialidad de *Fitzroya cupressoides* para reconstrucciones climáticas durante el Holoceno en Chile y Argentina. Revista Chilena de Historia Natural, 67: 443-451.

Lara, A., C. Donoso & J. C. Aravena, 1996. La conservación del bosque nativo de Chile: problemas y desafíos. Pages 335-362. *in* J. J. Armesto, C. Villagrán & M. K. Arroyo (ed.). Ecología de los Bosques Nativos de Chile. Editorial Universitaria, Santiago.

Lusk, C. H., 1996. Gradient analysis and disturbance history of temperate rain forests of the coast range summit plateau, Valdivia, Chile. Revista Chilena de Historia Natural, 69: 401-411.

Markgraf, V. & L. Anderson., 1994. Fire history of Patagonia: Climate *versus* human cause. Revista do Instituto Geográfico do Sao Paulo, 15: 35-47.

Neira E., 1995. Desarrollo de cronologías para alerce (*Fitzroya cupressoides*) en las Cordilleras de la Costa y de los Andes. Thesis. Facultad de Ciencias Forestales. Universidad Austral de Chile, Valdivia.

Parker, T. & C. Donoso, 1993. Natural regeneration of *Fitzroya cupressoides* in Chile and Argentina. Forest Ecology and Management, 59: 63-85.

Peralta, M., M. Ibarra & E. Oyanedel, 1982. Suelos del tipo forestal alerce. Ciencias Forestales, 2: 39-60.

Philippi, R. A., 1865. Escursión botánica en Valdivia desde Las Trancas en el Departamento de La Unión a través de la Cordillera de la Costa. Anales Universidad de Chile, 27: 289-351.

Ramírez, C. & M. Riveros, 1975. Los alerzales de Cordillera Pelada: Flora y fitosociología. Medio Ambiente, 1: 4-13.

Schmithüsen, J., 1960. Die Nadelholzer in den Waldgesellschaften der Südelichen Anden. Vegetatio, 10: 313-327.

Schulman, E., 1956. Dendroclimatic change in semiarid America. University of Arizona Press, Tucson, Arizona.

Silla, F., 1997. Dinámica regenerativa del alerce (*Fitzroya cupressoides*) de la Depresión Intermedia. Thesis. Facultad de Ciencias. Universidad Austral de Chile, Valdivia.

Stokes, M. A. & T. L. Smiley, 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois.

Veblen, T. T., 1992. Regeneration dynamics. Pages 152-187, *in:* D.C. Glenn-Lewin, R.K. Peet & T.T Veblen (ed.). Plant Succession: Theory and Prediction. Chapman and Hall, London.

Veblen, T. T., R. J. Delmastro & J. E. Schlatter, 1976. The conservation of *Fitzroya cupressoides* and its environment in southern Chile. Environmental Conservation, 3 : 291-301.

Veblen, T. T. & D. H. Ashton, 1982. The regeneration status of *Fitzroya cupressoides* in the Cordillera Pelada, Chile. Biological Conservation, 23: 141-161.

Veblen, T. T. & D. C. Lorenz, 1988. Recent vegetation changes along the forest/steppe ecotone in northern Patagonia. Annals of the Association of American Geographers, 78: 93-111.

Veblen, T. T. & V. Markgraf, 1988. Steppe expansion in Patagonia. Quaternary Research, 30: 331-338.

Veblen, T. T., K. S. Hadley, M. S. Reid & A. J. Rebertus, 1991. Methods of detecting past spruce beetle outbreaks in Rocky Mountain subalpine forests. Canadian Journal of Forestry Research, 21: 242-254.

Veblen, T. T., B. R. Burns, T. Kitzberger, A. Lara & R. Villalba, 1995. The ecology of conifers of southern South America. Pages 120-155 *in:* N. J. Enright & R. S. Hill (eds.). Ecology of the Southern Conifers, Melbourne University Press, Melbourne.

Villagrán, C., J. Varela, H. Fuenzalida, H. Veit, J. Armesto & J. C. Aravena, 1993. Geomorphological and vegetational background for the analysis of the Quaternary of the Chilean Lake District. Pages 1-50 *in* C. Villagrán (ed.). The Quaternary of the Lake District of Southern Chile. Santiago.

Villalba, R., 1990. Climatic fluctuations in northern Patagonia during the last 1000 years as inferred from tree-ring records. Quaternary Research, 34: 346-360.

Villalba, R., J. A. Boninsegna, A. Lara, T. T. Veblen, F. A. Roig, J. C. Aravena & A. Ripalta, 1996. Interdecadal climatic variations in millennial temperature reconstructions from southern South America. Pages 161-189 *in:* P. D. Jones, R. S. Bradley & J. Jouzel (ed.). Climatic Variations and Forcing Mechanisms of the Last 2000 Years, NATO ASI Series, Vol. 141, Springer Verlag, Berlin.

Villalba, R. & T. T. Veblen, 1997. Improving estimates of total tree ages based on increment core samples. Écoscience, 4: 534 - 542.

Wilhelm, E. J., Jr., 1968. Fire ecology of the Valdivian rain forest. Pages 55-10 *in* Proceedings 8th Tall Timbers Fire Ecology Conference. Tallahasee, Florida.