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Dendroecological analysis of a *Fitzroya cupressoides* and a *Nothofagus nitida* stand in the Cordillera Pelada, Chile

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Abstract

Lumbering of *Fitzroya* cupressoides in Chile began in 1599 and continued until 1976, when the species was declared a national monument and cutting of live trees was prohibited. Today, F. cupressoides is threatened; many of the remaining stands in the coastal range appear to be declining, with a predominance of standing dead stems and patchy, sparse regeneration. We performed tree-ring analysis on a *F*. cupressoides stand and a nearby *Nothofagus* nitidu stand, in the Cordillera Pelada. of coastal Chile (40°S) in order to examine the ecological history of two stands in the montane forest. Our analysis demonstrates that the *F*. cupressoides stand has undergone several periods of growth release and disturbance; the last 34 years of the chronology show a trend of increasing growth. In contrast, after 1865 radial growth of the N. nitida stand is fairly constant and steady. Radial growth of these two species is highly correlated with spring rainfall. November rainfall of the current growing season proved to be the best growth predictor of *F*. cupressoides, whereas current June and December rain of the past growing season best predicted growth of N. nitidu. Although episodic disturbances have occurred, the chronologies demonstrated that these stands are vigorous, despite the presence of dead stands nearby. These results do not support the idea that climatic deterioration is responsible for the decline of F. cupressoides during the past 77 years.

La tala de F. cupressoides en Chile empezó en 1599 y continuó hasta 1976, cuando la especie fue declarada monumento nacionál y la corta de arboles vivos fue prohibida. Esta especie es hoy considerada vulnerable. Muchos rodales que subsisten en las cumbres de la cordillera de la costa (40-42°S) parecen estar en declinación con una predominancia de individuos muertos en pie. La regeneracidn de F. cupressoides estálimitada a algunos rodales intervenidos. En este estudio se llevó a cabo un analisis de anillos de crecimiento de F. cupressoides y de N. nitida en dos rodales de la Cordillera Pelada (800-900 m), en la costa de Chile a 40°S, con el proposito de reconstruir la historia de estos bosques montanos en la cordillera de la costa. El analisis sugirió que el rodal de F. cupressoides ha sufrido varios períodos de liberación de crecimiento y perturbación. Los hltimos 34 aiios de la coronologia demuestran una tendencia de crecimiento alto. Por otra parte, despues de 1865, el crecimiento del rodal de N. nitidu es medianamente constante. El crecimiento de las dos especies se correlaciona fuertemente con las precipitaciones de primavera registradas en una estacidn al sureste del area de estudio. La lluvia del mes de noviembre del año anterior fue el mejor predictor de la cronologia de F. cupressoides, mientras que las

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lluvias de junio y diciembre del año actual y lalluvia de diciembre de los dos años anteriores predicen /a cronología de *N. nitida*. A pesar de la presencia de disturbios ocasionales, y la existencia de rodales vecinos compuestos de árboles muertos y de alta mortandad en rodales maduros. las cronologías demuestran que los rodales estudiados de F. *cupressoides* y de *N. nitida* están saludables. Estos resultados no apoyan la idea de que el deterioro del clima podría ser responsable por la reducción de F. *cupressoides* durante los últimos 77 años.©1998Elsevier Science B.V. All rights reserved.

Keywords Alerce: Climate effects: Coigue; Dendrochronology; Disturbance; Threatened species

1. Introduction

Structural changes that occur in an ecosystem over time are best investigated with frequently monitored permanent plots, but such data are unavailable from many forests. Most studies of forest succession have been of short duration and provide limited information about long-term changes. Dendrochronology can provide a retrospective method of obtaining knowledge about the history of a forest. Tree growth rings are available for previously unstudied forests, and tree rings provide a chronicle of the effects of climate on tree growth, and of standwide disturbances caused by fire, insects or pollution, for example (Cook et al., 1987; Veblen and Lorenz, 1987; Van Deusen, 1987, 1989; Veblen et al., 1991, 1992). A ring width chronology, the averaged ring width measurements from a number of trees from a site (Fritts, 1976), can provide information about the history of the forest. The common signal among the sampled trees indicates stand-level, year to year influences on radial growth (Cook et al., 1987).

In this study, we carried out tree-ring analysis of a Fitzroya cupressoides (Mol.) Johnson stand and a Nothofagus nitida (Phil.) Krasser stand in the Cordillera Pelada, the coastal range of Chile at 40°S, in order to better understand the ecological history of the forest community (Fig. 1). The objective of this study was to provide a long term historical growth record of the *E* cupressoides and N. nitida stands. E cupressoides, locally known as alerce, is a threatened species (CONAF, 1989). The predominance of standing dead stems, a phenomenon noted over a century ago by Philippi, 1865 and still poorly understood today, suggests that many *E* cupressoides stands in the coastal range are declining, although the time of death of trees in many stands is unknown. Knowledge of the history of this stand may

help assess the relative roles of human impact and climatic change in the current decline of *E cupressoides*.

F. cupressoides occurs in the Cordillera de la Costa to the northern part of the island of Chiloé, and in the Cordillera de los Andes between about $40^{\circ}30'$ and $43^{\circ}30'$ S (Ramirez and Riveros, 197.5; Lara, 1991). Because of the beauty and durability of its wood, E. cupressoides was one of the first species to be commercially exploited in Chile. On the island of Chiloé and the area around the estuary of Reloncavi, cutting of *E cupressoides* continued at a rapid rate from 1599 to the end of the 19th century (Fonck, 1896, in Donoso et al., 1990). By that time all the accessible forests near Puerto Montt and the estuary of Reloncavi had been nearly eliminated, and the *E* cupressoides forests of the central plain between Puerto Montt and Lake Llanquihue were cut or burned by colonists in the second half of the 19th century, during the German colonization (Armesto et al., 1995). Beginning in 1964, protection of the remaining *F. cupressoides* forests began, but considerable lumbering continued until 1976, when the species was declared a natural monument, and cutting was prohibited (Donoso et al., 1990).

Little is known about the history of disturbance in these forests. Regeneration of *E cupressoides* is patchy and inadequate in some areas; it seems to be limited to areas with low tree cover or large disturbed areas, and is extremely poor after clearcutting followed by fire or grazing (Veblen and Ashton, 1982; Lara, 1991; Donoso et al., 1993; Paez and Armesto, unpublished data). Regeneration is completely lacking in old-growth stands on the coastal range. In the Cordillera Pelada, disturbed areas appear to have been created by human-set fires, although natural fires may have also been important in the past. Extensive patches of standing, bleached dead *E cupressoides* common in many areas of the



Fig. 1. Location of the Cordillera Pelada in the southeastern section of the province of Valdivia, Chile. Shaded areas represent destroyed forest or bare ground

Cordillera Pelada, side by side with green patches, could be the result of such disturbance. Exploitation of standing dead stems is still legal, even though the logging of dead *F. cupressoides* may severely impair the possibility of natural regeneration because of interference produced by logging debris (Donoso et al., 1993).

Lara and Villalba (1993) suggested that the species' longevity makes it very valuable for dendroecological studies (long chronologies possible), and increases the reason to protect it. Boninsegna and Holmes (1985) were the first to successfully crossdate *F. cupressoides* and develop a tree-ring chronology. Villalba (1990) and Villalba et al. (1990) used an *F. cupressoides* growth chronology from the Patagonian Andes in Argentina to develop a 1120year reconstruction of summer temperatures. Lara and Villalba (1993) used *F. cupressoides* tree-ring records from southern Chile to estimate summer temperature for the past 3622 years.

N. nitidu is distributed from below 38°S latitude

northward along the Chilean coast and up the river valleys into the high cordilleras in northern Llanguihue (Chudnoff, 1984). Regeneration of N. nitida is dependent on large scale disturbances and canopy gaps created primarily by landslides and multiple tree falls (Armesto et al., 1995). Nothofugus wood is commercially valued as an all-purpose timber in Chile, but since it is more readily available in low elevation forests than F. cupressoides, the high elevation stands have not been subjected to file or to large scale logging operations. N. nitida has not been logged or impacted by humans in montane coastal forests, in contrast to what happened with F. cupressoides. The wood is of medium hardness and weight, straight grained and fine textured. Nothofagus species are capable of living 200 + years and generally have distinct growth rings (Kribs, 1968). This makes N. nitidu valuable for dendroecological analysis and for comparison with F. cupressoides forests, that have been more disturbed by humans in the recent past.

1.1. Material studied, area descriptions, methods, techniques

F.cupressoides sampling was conducted within the boundaries of Monumento Nacional Alerce Costero $(40^{\circ}20' \text{ S}, 73^{\circ}30' \text{ W})$ a 2308 ha forest preserve (Fig. 3), located above 800 m elevation in the Cordillera Pelada, the coastal range north of Valdivia, Chile $(39^{\circ}48'S)$. The study area receives more than 3000 mm of annual rainfall (Veblen and Ashton, 1982), with 40% concentrated between June and August (winter). Mean annual temperatures are usually mild, due to the strong oceanic influence, although local records are lacking. January (midsummer) and July (mid-winter) mean temperatures in Rio Bueno $(40^{\circ}18'S; 58 \text{ m elevation})$ are 16.4 and 6.9°C, respectively. High elevations of the coastal range may receive some precipitation as snow during July and August. These coastal forests are far from industrial sources of air pollution that could cause forest decline, and receive uncontaminated precipitation.

On the summit plateau, (800-1000 m), stands dominated by F. cupressoides (Cupressaceae), grow on heavily podzolized soils (Veblen and Ashton, 1982). These stands have an open canopy 15-20 m in height on flat, often poorly drained, sites. The shrub layer is formed by Desfontainea spinosa R. and Pav., Philesia magellanica Gmel., and extensive patches of the bamboo, Chusquea sp. Below 700 m, on steeper slopes and deeper soils, F. cupressoides forests are replaced by a mixed forest, with a denser and taller (>20 m) canopy of N. *nitida* (Fagaceae), Drimys winteri Forst. (Winteraceae), and the conifers Podocarpus nubigenus Lindl. and Saxegothaea conspicua Lindl. (both Podocarpaceae). Weinmannia tricosperma Cav. (Cunioniaceae) is occasionally present in the mixed forest.

Away from the meadow areas on the summit plateau, at around 900 m, was a nearly pure stand of alerce, 20 ha or more in size, suitable for **den**drochronological study. The topography was gently sloping and the understory was **shrubby** in places, but in general fairly open. The forest floor was carpeted in vegetation. Many of the trees had **epi**phytes growing on the trunks, attesting to the high humidity of the area. We saw no evidence of recent fires in the stand and the trees appeared healthy. Below the summit on a fairly flat area of a southeast facing slope of the cordillera, at around 650 m, was a mixed species stand where a significant proportion (15-20%) of the canopy trees were *N.nitida*. This stand had a fairly closed canopy, and a stream running through it.

We cored 30 trees per stand and took two cores per tree, 180" from each other. In transit. one package was damaged so we ended up with JO cores from 28 F. cupressoides trees and 42 cores from 24 N. nitida trees. Increment cores were extracted at breast height (1.37 m). Trees were cored parallel to the contour. The F. cupressoides stand appeared fairly homogeneous so we chose sample trees more or less uniformly spread across the central 5 ha of the site. In the mixed species stand we walked a more or less straight transect heading northwest into the stand. About every 15 m we stopped and looked for a N. nitida tree within about 3 m of the spot. If a suitable tree was not found (we bypassed intermediate and suppressed crown class trees, and trees with obvious defects), we went another 15 m and so on. We assumed this gave us a representative cross-section of the stand.

The cores were air dried, mounted on wooden blocks, and hand sanded with three grades of sandpaper. Cores were then inspected, with the best 34 cores of F. cupressoides (28 trees) and 33 cores of N. nitida (24 trees) selected for measurement and crossdating. Cores with indistinct rings or with several breaks or rotten spots were eliminated (six F. cupressoides and nine N. nitida cores). Ring widths were measured to 0.001 mm using software developed at the Institute for Quantitative Studies (Van Deusen, 1993). Reliance on marker rings, interactive graphics, and correlations of ring patterns helped establish correct ring sequences, and dating was assisted and checked by the use of the program XCHECK (Van Deusen, 1993). Table 1 lists the correlation of each core against the others, and provides the crossdated core age, for each species. The oldest F. cupressoides was 398 years and the youngest was 143 years; the oldest and youngest N. nitida were 231 and 35 years, respectively. For purposes of looking at the long term stand growth pattern and for detecting periods of disturbance/release, a horizontal straight line standardization is recommended by Veblen et al. (1991, 1992). While

F. cupressoides				N. nitida			
Core	Correlation	Age	Starting year	Core	Correlation	Age	Starting year
<u>}</u> ×	0.28	399	1593	27	0.19	232	1760
-	0.41	265	1727	26	019	224	1768
10	(+.	263	1729	11	0 25	170	1822
.	1.2.	262	i730	24	0.21	l-11	1851
	s 1	261	1731	10	0 44	131	1861
	0.58	259	1733	18	0.24	129	1863
15	41.57	259	1733	17	0.41	126	1866
23	6.54	257	1735	29	0 '3	120	1872
1.1	2 G	`5 ∔	17.58	33	0.19	118	1874
	. 1	201	. +1	15	0.29	116	1876
•	0.57	-51	1741	4	0.24	111	1881
ŝ.	0.27	_ 5Ú	1742	Ó	0.29	106	1886
X_{1}^{*}	5 1 7	249	1743	23	0.34	L04	1888
24	(35	247	1745	-	0.27	101	1891
2	0.45	<u>-</u> +0	I746	22	0.20	101	1891
	5.5		1750	19	0.22	99	1893
1.5	641	240	1752	25	0 39	92	1900
21	0.12	2.40	1752	28	0.26	92	1900
27	$D \neq j$	240	1752	30	0 20	91	1901
31	0.54	240	1752	20	0.23	89	1903
1	0.+0	237	1755	14	0.41	89	1903
10	0.54	235	1757	16	0.27	81	1911
9	0.53	234	1758	5	0.25	79	1913
30	0.39	230	1'62	1	0.38	72	1920
34	0.22	230	1762	9	0.36	69	1923
7	0.29	227	1765	8	0.28	65	1927
13	0.59	227	1765	r	0.38	62	1930
53	0.25	2.27	1765	13	0.20	60	1932
2	0.43	218	1774	21	0.51	59	1933
22	0.43	212	1780	31	0.35	57	1935
26	0.45	195	1797	3	0.49	38	1954
14	0.37	177	1815	32	0.52	38	1954
10	0.4 4	159	1833	12	0.24	36	1956
)5	(1)	1.14	18.18				

Table 1 Correlations of core i with all other cores, tree age, and starting year, by species

reducing the within and among core variance, the age-related effect is retained. Let MSRW represent mean standardized ring width. Percent change in radial growth is computed as MSRW – $tag(MSRW)/tag(MSRW) \times 100$, where lag means an earlier value. A growth release was defined as a 40% or greater change in MSRW sustained for at least 5 years. We computed and examined tables of percent change for lags from 1 to 5 years as an aid in interpreting the graphs of the horizontal standardized chronologies.

Each chronology was analyzed to determine patterns of growth with available weather data. Graybill (1982) postulated that the following components form the ring widths of a single tree at time t:

$$R(t) = C_{t} + B_{t} + D1_{t} + D2_{t} + e_{t}, \qquad (1)$$

where C, is the climate component at time t, common to all trees; B_t is the biological growth trend; Dl, is a disturbance signal unique to the individual tree; $D2_t$ is a disturbance signal common to most or all individuals (stand level disturbances) and e, is (random) noise. It is crucial to remove long-term trends, unique to each tree, so that most of the remaining variance is due to the macrosignals C and D2 that all trees share. Part of this common signal

should be due to climatic factors more or less favorable to expected growth (Van Deusen. 1988).

For this analysis we standardized the cores by using the first difference of the inverse hypersine (similar to log transformation) of the ring widths in order to remove the biological growth trend (Van Deusen. 1987). Each series was then assumed to be composed of two macrosignals (C and D2) and two microsignals (D1 and e) which were treated as noise. Hence. the standardized ring widths were depicted as a linear function of climate variables, a common disturbance variable and a random component. This method of standardizing the ring widths removes the age-related trend and puts trees of different ages on equal footing; thus, the computed average is not dominated by the faster growing trees. This removes from the ring width series a lot of the low frequency variation and leaves the high frequency variation (stand growth). The variance of the early years for both chronologies is unstable, because the chronologies were composed of one or a few cores during the earliest years, and those trees were young and growing vigorously.

After standardization, the program ALLREGS (Van Deusen, 1993) was used to screen many climate models, using weather variables for the current year and 2 previous years. Mean monthly temperature and/or total monthly rainfall were available from Puerto Montt (41.42°S and 73.08°W), La Unión (40.30°S and 73.00°W), Punta Galera (40.00°S and 73.70°W), and Valdivia (39.80°S and 73.20°W). After ALLREGS identified the key weather variables, we used the program DYNAOLS (Van Deusen, 1993) to fit model 1 to the *F* cupressoides and N. *nitida* chronologies.

2. Results

Most of the *E* cupressoides trees reached breast height between 1730 to 1760 (Table 1 and Fig. 2a). Only one tree predates 1727. Starting in 1730 initial growth rates were high, as expected for trees colonizing an open site following a large scale disturbance, either logging or fire. A gradual radial growth decline occurred from 1751 to 1821. This pattern probably reflects some ageing effects but most likely represents stand closure (competition effects). After



Fig. 2. (a) Mean horizontal line standardized *F. cupressoides* ring-width chronology illustrating growth and disturbance patterns. Standardization was achieved by dividing **observed ring** widths by the mean ring-width value for each tree. Graph of core sample size (n) appears below chronology. (b) The standardized (first difference of the inverse hypersinetransformation) and then averaged chronology of the *F. cupressoides* tree-ring series for 1594-1991. Units on y axes are 0.001 mm.

1821 there is a dramatic surge in growth indicating some major disturbance occurred (selective logging, **blowdown** or fire) which thinned the stand and released the surviving trees from competition. Within 3 years the radial growth rate increased by 52% and by 1827 the percent change was 86%. A second gradual decline in growth occurred between 1836 and 1896. Another release occurred, though not as dramatic as the first release, and by 1899 radial growth rate was up 44%. After 1908, a sharp decline occurred until 1918. A seemingly cyclical pattern sets up with an increase to 1934 then a decline until 1945, increasing until 1952 and declining until 1957, with a gradual increasing trend over the next 34 years to 1991. where the chronology ends. The rise in the chronology after 1918 represents a third release in the stand. with the growth rate up by 46% within 3 years.

Several strong El Niño events occurred between 1900 and 199 1(Diaz and Markgraf, 1992). We examined the *F. cupressoides* chronology for changes in growth during these years, or the year following, but no clear pattern emerged in the chronology as a result of El Niño events.

C

Tree ages for N. *nitida* are more variable, as is typical of mixed species uneven-aged stands dependent on gap regeneration (Table 1 and Fig. 4a). In 1822 a third tree enters the chronology, then a fourth and fifth tree enter in 185 1 and 1861, respectively. The chronology during this 40 year time period indicates that the oldest trees did not initially grow rapidly. Thus, this stand is not a first generation post disturbance stand like the *E cupressoides* stand. Most of the trees enter the chronology after 1880 with little variation in the long term growth trend, in contrast to the *E cupressoides* chronology.

Only precipitation data from 193 1- 1960 were available from La Union, but November, February and June rain of the current growth season from that location proved to be the best predictors of the F. cupressoides chronology. The variation explained in the transformed chronology was 60% ($R^2 = 0.60$) and the root mean square error (RMSE) was 0.09 (p < 0.001). The individual correlations between the transformed chronology and the climate variables was - 0.30 for February rain, 0.05 for June rain, and 0.65 for November rain of the current growth season. In contrast, the variation explained by the temperature and precipitation at Valdivia was only 10% $(R^2 = 0.10)$ and not significant; the Puerto Montt and Punta Galera data gave similar results. Fig. 2b shows the transformed average chronology of the *E*. cupressoides ring widths over time. Because we used the first difference of the ring widths, the transformed chronology shows a poor year following years in which growth is above average. The observed and expected values of the ring widths over time are shown in Fig. 3a. The predicted growth was obtained from the program DYNAOLS with the climate variables of November, February and June rain of the current growth season. The observed and



Fig. 3. (a) The observed (solid) vs. predicted (dashed) value of the *F. cupressoides* data. The expected values were calculated by the program DYNAOLS with the climate variables of current February and June rainfall and November ram lagged 1 year. The observed and predicted values are similar and almost always run in the same direction. (b) The smoothed residuals from using the program DYNAOLS with the climate variables current February and June rainfall and November rain of the previous year The smoothed residuals will yield a **positive** value when the model underpredicts growth and a negative value when the model over-predicts. Units on y axes are 0.001 mm.

predicted values are similar; the smoothed residuals (Fig. 3b) yield a positive value when the model underpredicts ring width and a negative value when predicted growth is greater than observed. Smoothing involves using information that is available up to time t as well as information produced after time t (Anderson and Moore, 1979).

As with *E* cupressoides, the La Unión weather data correlated the best with the transformed N. *nitida* chronology (Fig. 4b). June and December rain of the current year and December rain lagged by one



Fig. 4. (a) Mean horizontal line standardized *N.nitida* ring-width chronology Illustrating growth and disturbance patterns. Standardization was achieved by dividing observed ring widths by the mean ring-width value for each tree. (b) The standardized average chronology of the N. *nitida* tree-ring series.

growth season were the best predictor variables. A total of 46% ($R^2 = 0.46$) of the variation in the chronology was explained by the precipitation data, and the RMSE was 0.10 (p = 0.002). The individual correlations between the transformed chronology and the climate variables were -0.36 for June rain, 0.29 for December rain and 0.37 for December rain of the past growth season.

3. Discussion

Examining the *F. cupressoides* and N. *nitida* ring-width sequences graphically over time in terms

of the climate variables can reveal long-term growth trends. November (spring) rainfall of the current growth season proved to predict the *Ecupressoides* chronology better than other months of the current or past growth season. This is springtime in the southem hemisphere, and the current year's growth begins during the previous year. It is not surprising that spring rain is important in predicting the growth of E cupressoides. Growth in this month apparently has a significant Influence on the variation in total annual growth. These results are similar to those reported by Phipps (1961a, Phipps, 1961b) who found that (based on weekly dendrometer measurements) as much as 80% of radial growth of several deciduous species in Ohio occurs during late spring (mid May and late June).

Although the months selected best predicted ring widths over all the years (November. February and June rain of the current growth season), they may not have been the best for any individual growth season. Rainfall and temperature during other months also influenced growth. December rain of the current and past growth season, and June current season rain predicted the N. nitida chronology best, but N. *nitida* does not have as strong a climate signal as **F**. **cupressoides** as evidenced by its lower R^2 (0.46 vs. 0.60) but essentially same RMSE (0.10 vs. 0.09) from model 1. Because bud formation, storage of photosynthates, formation of growth hormones and other growth processes occur the year before radial growth develops, previous variations in climate can affect the ring width of the current year (D'Arrigo and Jacoby, 1992).

The horizontal line transformed chronology (Fig. 2a) demonstrates that this *E cupressoides* stand has undergone several periods of growth release and disturbance giving the growth trend a roller coaster appearance. The pattern of juvenile growth and gradual decrease from 1730 to 1821 probably reflects some ageing effects but most likely represents stand closure (competition effects). The striking surge in growth after 1821 indicates some major disturbance occurred which thinned the stand and released the surviving trees from competition. *E cupressoides* wood persists for well over a century with little decomposition, but there is no evidence of logging (stumps) or of blowdown (boles on the ground); most likely, fire caused the releases.

The forests of the cordillera are affected by severe cyclonic storms and were subjected to anthropogenic fires and cutting (Heusser, 1982) prior to the formation of the Monumento Natural Alerce Costero. The last 34 years of the *F. cupressoides* chronology show a trend of increasing growth which coincides with the exclusion of direct human impact in the stand (protection of the forests began in 1964). but is not necessarily caused by it. The horizontal line transformed chronology of N. nitidu (Fig. 4a), from mid-elevation in the cordillera. indicates some type of disturbance around 1865. After that there is a strong recovery and a more-or-less flat long term growth trend, which (as opposed to the short term year to year sawtooth variation typical of all tree chronologies) is fairly constant and steady, in contrast to the cycling observed in the *E. cupressoides* chronology. The growth trend indicates a healthy stand undergoing natural processes in uneven-aged mixed species stands. Although the chronologies reveal that these stands of *E. cupressoides* and N. nitidu are generally healthy, in nearby stands some or all of the F. cupressoides trees have died standing.

Heusser (1982) identified fossil pollen in three cushion bogs of the Cordillera Pelada. He found E cupressoides type pollen in the Cordillera Pelada diagrams after about 6500 years Before Present (BP), when a regional rise in precipitation took place (precipitation reconstructed from fossil pollen data). Although fire and exploitation by European colonists have accentuated the species' decreasing numbers in recent centuries (Veblen et al., 1976), evidence from three pollen records at the town of Alerce demonstrated that the greatest proportion of *E cupres*soides pollen was present during the Holocene around 4000 years BP, and that *F. cupressoides* pollen has gradually declined since then. Heusser and Streeter (1980) postulated that the decline began before the arrival of the Europeans and likely was caused by the estimated reduction in precipitation. Heusser (1982) also suggested that past rainfall in the Cordillera Pelada was distributed more uniformly through the year, with increased humidity and cloudiness and lower temperature, and without a summer drought. A decrease in precipitation since the middle of the 19th century was documented by instrumental records at Valdivia about 40 km north-

west of the cordillera (Veblen et al., 1976). However, Heusser (1982) reconstructed average annual precipitation and average January temperature at the town of Alerce (150 km southeast of the study area) $(41^{\circ}25'S, 72^{\circ}54'W)$, and suggested that temperature there has decreased and precipitation has increased since approximately 1920, after an increase in temperature and decrease in precipitation that continually worsened during the preceding 350 years. The decline in temperature in Puerto Montt since the early 1900's has been documented by Aceituno et al. (1993). Our analysis demonstrated that growth of \boldsymbol{F} cupressoides in the stand we studied (at 900 m) was weakly correlated with temperature and precipitation at Valdivia (sea level). and highly correlated with precipitation at La Union (approximately 30 km southeast of the study area).

Villagran (1991) reports that *E cupressoides* and N. *nitidu* forests were present at mid elevations on the coastal range between 12,500 and 9500 YBP (from the beginning of the Holocene). Hence, decline of *E cupressoides* pollen in profiles from the Lake district may indicate that the species was migrating to higher elevations, both in the Andes and coastal ranges rather than declining regionally. Pollen profiles show that *E cupressoides* has colonized the Andes in the past 3000 years (Villagran, 1991).

It is surprising that the *F. cupressoides* stand has been healthy, with no long term decline, while dead stands and stands of mixed dead and live trees occur nearby in the Cordillera Pelada and on Chiloe Island (Armesto et al., 1995). In some of the dead stands, there is evidence of recent fire, but in others it is not obvious why the trees have died. There are no obvious symptoms of insects or disease, and no nearby sources of pollution. It appears that weather conditions at Cordillera Pelada are more similar to conditions to the southeast than to those at Valdivia. The long decrease in precipitation at the town of Alerce began to reverse 77 years ago; perhaps some of the trees that died are exhibiting a delayed reaction to the previous unfavorable conditions. Because dendrochronology does not show any evidence for a decline in growth rates associated with decreased precipitation, some other factors must be responsible for the observed dying stands. Delayed reaction to previously unfavorable conditions could be a plausible alternative explanation, but climatic deterioration is not supported by the analysis of N. *nitida* in a nearby stand.

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