Gradient analysis and disturbance history of temperate rain forests of the coast range summit plateau, Valdivia, Chile

Análisis de gradientes e historia de perturbación de bosques de las cimas de la Cordillera de la Costa, Valdivia, Chile

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ABSTRACT

Detrended correspondence analysis (DCA) of overstorey floristics was used to examine relationships between environmental and compositional gradients in rainforest communities on the summit plateau of the coastal ranges south of Valdivia, Chile. Edaphic, topographic and stand history data were gathered at each site, to examine the relative importance of site and successional influences on stand composition. Variation in overstorey composition of mature forest stands on the summit plateau was associated primarily with collinear gradients of soil drainage and nitrogen status. Edaphic and floristic gradients were rather weakly linked to topographic position, reflecting the influences of spatial variation in parent material on soil development. The abundance of even-aged stands on the coastal range tops, and evidence of both fire and stand blowdown, indicates that local pre-Hispanic disturbance regimes may have differed appreciably from those prevailing at lower altitudes in the same range. There was also evidence of spatial variation in disturbance regimes within the study area. Although minimum stand age did not vary systematically in relation to edaphic gradients, the evidence points to fire as the dominant agent of stand initiation on low fertility sites, whereas stand blowdown appeared to be more common on higher fertility sites.

Key words: disturbance regime, *Fitzroya cupressoides*, *Nothofagus*, edaphic gradients, succession.

RESUMEN

En comunidades boscosas de las cimas de la Cordillera de la Costa, Valdivia, Chile, se estudiaron las relaciones entre los gradientes ambientales y florísticos, aplicando el análisis de correspondencia con corrección de tendencia (DCA) a datos de especies del dosel arbóreo. Datos edáficos, topográficos y de edad de los rodales fueron obtenidos de cada parcela, para examinar las influencias relativas del sitio y de sucesión sobre la composición del dosel. Se determinó que la variación en la composición de los rodales maduros está asociada, principalmente, con gradientes colineales de drenaje y contenido de nitrógeno del suelo. Los gradientes edáficos y florísticos están débilmente vinculados con la posición topográfica, reflejando una influencia de variación espacial de la roca madre en el desarrollo del suelo. La abundancia de rodales coetáneos, y las evidencias de disturbios por vientos e incendios, sugieren que los regímenes de perturbación en las cimas antes del comienzo de la explotación de los bosques eran marcadamente diferentes de aquellos que prevalecieron en bosques de elevaciones menores en la misma Cordillera. No obstante, también se encontró evidencia de variación de los regímenes de perturbación dentro del área de estudio. Aunque no se detectó variación sistemática en la edad de los rodales en relación a los gradientes edáficos, se observó evidencia de incendios principalmente en los sitios poco fértiles, mientras evidencias de destrucción de rodales por tormentas de viento eran comunes en sitios de fertilidad alta y mediana.

Palabras clave: *Fitzroya cupressoides*, gradiente edáfico, *Nothofagus*, régimen de perturbación, sucesión.

INTRODUCTION

Landscape-level vegetation patterns are commonly interpreted in relation to complex gradients of climatic, topographic and edaphic factors (Whittaker 1956, Peet 1981). However, in most forest biomes, succession produces temporal shifts in species composition; as a result, if disturbance history varies throughout the area studied, gradient studies based only on site factors may have limited explanatory power (Harmon et al. 1983, Allen & Peet 1990). Disentangling the relative influences of site and successional effects on stand structure and composition is facilitated by stand history data, which in

temperate forests can often be obtained from tree-ring studies (e.g. Lorimer 1985). Alternatively, size-class ordination can be used to identify succesional relationships between vegetation mosaic units (Goff & Zedler 1972, Franklin et al. 1993).

In the Mediterranean-climate region of central Chile, as in other semi-arid and sub-humid regions of the world (Allen & Peet 1990), relief and exposition have been shown to be major determinants of local vegetation patterns, through their effects on site moisture balance and evapo-transpiration (Armesto & Martínez 1978, Rundel 1981). However, there has been little quantitative study of the environmental correlates of fine-scale vegetation patterns in the temperate rainforest region of southern Chile. Fine-scale compositional variation is also often tightly linked to topography in humid temperate regions throughout the world (Whittaker 1956, Gagnon & Bradfield 1987, Burns & Leathwick 1996), reflecting topographic control of soil physical and chemical properties (Jenny 1980) and/or disturbance regimes (Harmon et al. 1983).

In this paper I explore the influences of topographic, edaphic and historic parameters on composition of rainforest communities on the summit plateau of the coastal ranges south of Valdivia (Cordillera Pelada). The choice of this area was motivated by the diversity of the mosaic of vegetation types found within a narrow altitudinal belt on the range summits. The environmental correlates of the vegetation mosaic have not been examined by quantitative analyses, although Veblen & Ashton (1982) suggested that the conifer *Fitzroya cupressoides* (Mol.) Johnst. (Cupressaceae) is associated mainly with shallow podzol soils, and that except at the highest altitudes, more fertile brown earths are generally occupied by mixed evergreen forest dominated by *Nothofagus nitida* (Phil.) Krasser (Fagaceae), *Saxegothaea conspicua* Lindl. (Podocarpaceae) and *Laureliopsis philippiana* (Looser) Schodde (Monimiaceae).

Large areas of forest on the range summit were destroyed or damaged by human-set fires in the 19th and 20th centuries, and during the same period *Fitzroya cupressoides* has been widely exploited for its highly-prized timber (Ramirez & Riveros 1975,

Veblen & Ashton 1982). It is clear that massive disturbance of the summit plateau forests also occurred before this period, although the causes are unclear. For example, Philippi (1865) described large areas of dead standing *F. cupressoides* and vigorous regeneration on the range summit in the mid-19th century, without being able to ascertain the causes or date of the implied disturbance. Even-aged stands are widespread in the present summit plateau forests, and some of these clearly predate the definitive establishment of Hispanic control over southern Chile, a phase of expansion which began ca. 1750 and culminated in the clearing of large areas of forest in the mid-19th century (Guarda 1973). Therefore, coarse-scale disturbances may have had an important role in shaping forest pattern on the summit plateau even before Hispanic exploitation of the area.

The main questions to be addressed in this paper are: (1) how does stand composition at a given age vary in relation to geomorphic and edaphic factors? (2) What role has spatial variation in pre-Hispanic disturbance history played in shaping the present forest pattern? This second question is important to the understanding of the vegetation mosaic, as topographic variation in disturbance regimes is a potentially important influence on floristic composition (Peet 1981, Harmon et al. 1983).

STUDY AREA

The range summit consists of an undulating plateau at 800-1050 m asl, formed from Paleozoic micaschists with a variable quartz content (Oyarzún 1985). Soils vary considerably over short distances in depth, texture, horizon development, and drainage, ranging from well-drained brown loams up to 60 cm deep, to shallow gley podzols. In addition to bog communities and *Nothofagus antarctica* (G. Forster) Oerst. woodlands, the upper altitude vegetation of the range includes forest stands dominated variously by *Fitzroya cupressoides*, *Nothofagus nitida*, *Weinmannia trichosperma* Cav. (Cunionaceae), *Saxegothaea conspicua* and *Laureliopsis philippiana*. Other common canopy and understorey tree species include *Amomyrtus*

luma (Mol.) Legr. et Kaus. (Myrtaceae), *Drimys winteri* J.R. et G. Forster (Winteraceae), *Myrceugenia chrysocarpa* (Berg) Kausel (Myrtaceae), *Nothofagus betuloides* (Mirb.) Oerst., *Podocarpus nubigena* Lindl. (Podocarpaceae), and *Pseudopanax laetevirens* (Gay) Franchet (Araliaceae).

The coastal ranges are characterized by a maritime, superhumid temperate climate. Mean annual precipitation on the summits has been estimated at around 4000 mm, including occasional snowfalls between May and October, with a marked summer minimum (Almeyda & Saez 1958). No temperature records were available for the range summit.

METHODS

Vegetation sampling

A compact area of about 6 km² was sampled, comprising the Piedra del Indio summit (40° 12' S, 73° 26' E) and the upper reaches of the Lañinagual Stream. Vegetation was sampled on 43 0.1 ha plots in this area, all within a narrow altitudinal belt (800-940 m asl). Plots were sited systematically using a 250 m x 250 m grid on a 1: 50,000 scale topographic map. Only stands showing minimal evidence of logging or fire within the last 100 years were sampled, which meant that over 70% of potential plot sites within the study area were rejected. Only tall, closed forest communities were sampled, excluding bogs, and *Nothofagus antarctica* woodland on valley bottoms strongly affected by cold air ponding. Within each plot, the diameters of all woody stems > 2 m tall were measured at breast height. Nomenclature follows Marticorena & Quezada (1985).

Geomorphic and edaphic variables

Altitude of each plot was determined from a topographic map, and slope angle and aspect were measured in the field. A 1 to 5 scale has sometimes been used in gradient studies to quantify topographic position (1 = valley bottom, 5 = ridgetop) (e.g. Allen & Peet 1990). However, this scale proved difficult to apply to the peneplain landscape of the coastal range tops, which includes many flat or near-flat sites, but few sites that could be described as valley bottoms or ridgetops. Most sites therefore fitted into one of four topographic categories: concave slope, midslope, convex slope, flat or near-flat. These categories were used as a four-point topographic scale later in the interpretation of ordination axes (1 = concave slope, 4 = flat). A five-point index of exposure was derived from distance to opposite slope, estimated from the topographic map (1 = < 50 m; 2 = 50-200 m; 3 = 200-800 m; 4 = 800-3000 m; 5 = > 3000 m).

A soil auger was used to measure total soil depth to bedrock at 4 points evenly-spaced along the long (cross-slope) axis of each plot. At the same 4 points, samples of the uppermost 10-15 cm of mineral soil were extracted, after removing the organic horizons. The homogenized mineral soil samples from each site were analysed for several physical and chemical parameters at the Laboratorio de Análisis Foliar y de Suelos, Universidad de Talca: pH, % organic matter, total C, total N, C: N ratio, extractable P, extactable K, Mg & Ca, and % sand, silt & clay.

Soil drainage was assessed subjectively using a 3-point scale. Gleyed soils indicative of chronic waterlogging were scored as 1. Soils with mottling indicative of intermittent waterlogging were scored as 2, and those without appreciable mottling were scored as 3 (well-drained).

Stand age data

Ages of 5-8 canopy or emergent trees at each site were estimated from ring-counts on increment cores, as an approximation of time elapsed since stand-destroying disturbance. Cores were extracted as close to the ground as possible (usually below 50 cm), and no correction was made for time to grow to sampling height. 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 centre of the tree. Only cores including at least 70% of the geometric radius were used for age estimates.

Minimum stand age was usually defined as the greatest tree age determined from ring

counts. However, in stands which contained a few trees that were appreciably older than the main cohort, stand age was expressed as the age of the oldest tree found in the main cohort. In regions where the intervals between stand-destroying disturbances often exceed the lifespan of the longest-lived tree species, under-estimates of stand age are probable in old, uneven-aged stands, due to extinction of the cohort established after the previous coarse-scale disturbance event. However, this seems an unlikely scenario in the present study, due to the widespread presence of long-lived species such as *Fitzroya cupressoides* and *Saxegothaea conspicua*, and the evidence for frequent stand-destroying disturbances. In stands that appeared to be old and uneven-aged, age data were obtained preferentially from these species, in an attempt to minimize under-estimates.

Environmental and floristic gradients

Overstorey compositional variation was examined by detrended correspondence analysis (DCA), a widely-used multivariate technique that extracts dominant compositional gradients from a species-by-site matrix of abundance data (Hill & Gauch 1980). Numbers of overstorey stems (i.e. ≥ 10 cm dbh) of each species on each plot were used for the analysis, which was run with default options. Species represented on less than 5 plots were omitted.

In gradient studies it is often desirable to distinguish between site and successional influences on stand composition. To this end, Franklin et al. (1993) examined site-vegetation relationships by ordinating only stands "in compositional equilibrium", as determined by concordance of overstorey and understorey composition. Using this criterion, very few stands on the Cordillera Pelada summits could be considered to be in compositional equilibrium. Instead, I attempted to minimize the effects of stand age on site-vegetation relationships by running DCA only with stands between 200 and 400 years old (30 stands). This procedure gave markedly different species and site ordinations from earlier trials run with the full data set of 43 plots, including stands ranging from 130 to

770 yrs old.

The first two DCA axes were interpreted by examining correlations of plot scores with topographic, edaphic and stand age parameters. As several of the site parameters were non-normally distributed, and as two (drainage and exposure indices) were rank variables, non-parametric correlations were used. As north-south differences in exposition usually have much greater relevance to vegetation patterns than east-west differences, eastern and western deviations from the polar axis were both collapsed into the same scale of 0 (north) to 180 (south), in order to permit direct correlation of aspect with ordination axes.

Disturbance history

Non-parametric correlations were used to determine if minimum stand age (and hence, disturbance history) varied systematically in relation to topographic and edaphic gradients. As the interest was primarily in disturbance regimes prevailing before Hispanic settlement and exploitation of the area, these analyses were applied only to stands >200 years old (35 stands). Loss of information resulting from recent human modifications of the vegetation mosaic is probably an important source of error inestimation of pre-Hispanic disturbance frequencies. In particular, timber exploitation has selectively removed or damaged older stands of *F. cupressoides*, possibly resulting in under-estimates of return times for stand-destroying disturbances in *F. cupressoides* forests.

RESULTS

Axis interpretation: environmental and compositional gradients

The first two DCA axes accounted for 36% and 12% of the total variance of overstorey composition (Table 1).

Four poorly-defined clusters of plots are apparent when sites are ordinated on the first two DCA axes (Fig. 1). Stands in the first cluster from the left (low scores on both axes) were characterized by scattered to dense *Nothofagus nitida* over a subcanopy of

Axis	Eigenvalue variance	% of total % of total	Cumulative length (sd)	Gradient
1	0.543	35.8	35.8	2.65
2	0.180	11.8	47.6	2.19

Laurelia philippiana and *Saxegothaea conspicua*. A small group of plots with fairly low scores on axis 1 and high scores on axis 2 were characterized by *Weinmannia trichosperma* and *N. nitida* over *S. conspicua*. A dense cluster of plots with intermediate scores on both axes were characterized by *N. nitida* over *S. conspicua* and *Podocarpus nubigena*, and a group of plots with high scores on axis 1 were dominated by *Fitzroya cupressoides*.

Compositional variation along the first ordination axis was associated with soil fertility factors, which in turn appeared to be rather loosely linked to topography. DCA axis 1 was highly negatively correlated with several soil parameters (Table 2), most notably with with soil drainage (r = -0.82),

total nitrogen (-0.72), soil organic matter (-0.56), and depth (-0.55). The very strong correlation with drainage must be interpreted with caution, in view of the subjective nature of the assessment of this parameter. There were also weaker but statistically significant relationships with topographic position (r = 0.52), aspect (-0.43), and C:N ratio (-0.44). Low-scoring stands on axis 1 were therefore most frequently found on south-facing, concave slopes, and that high-scoring stands tended to occur on flat sites or on north-facing, convex slopes.

In the species ordination (Fig. 2), low first axis scores for *Amomyrtus luma* and especially *Laureliopsis philippiana* indicated that they were associated with well-drained, nitrogen-rich, deep soils, which were most commonly found on concave slopes. In contrast, the high scores of *Fitzroya cupressoides*, *Nothofagus betuloides* and *Drimys winteri* on DCA axis 1 identify them as species tolerant of infertile, poorly-drained and shallow soils, which were most frequently found on upper slopes and flat sites. *N. nitida*, with an intermediate score on axis 1, was found throughout the complete range of site conditions sampled in this study.
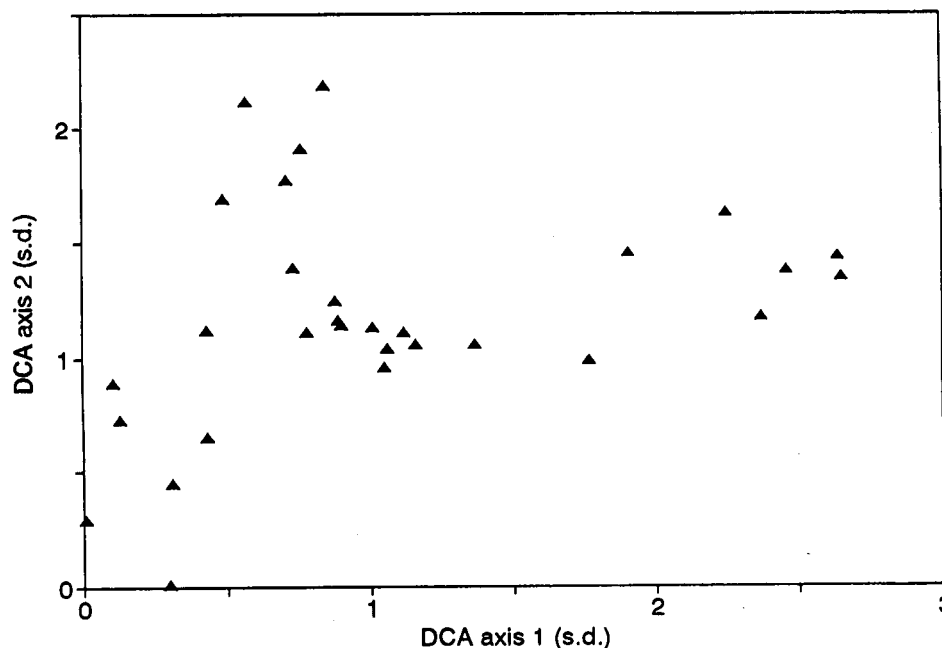

Fig. 1: DCA ordination of 30 stands (200-400 yrs old) from the Cordillera Pelada summit plateau.

Ordenamiento DCA de 30 rodales (200-400 años de edad) de las cimas de la Cordillera Pelada.

TABLE 2

Spearman rank correlations of plot scores
on DCA axes 1 & 2 with edaphic, topographic
and stand history parameters (n = 30).
Critical value (2-tail, 0.05) = +/- 0.37

Correlaciones no paramétricas de Spearman para los
ejes 1 y 2 del DCA, con parámetros edáficos, topográficos y
de historia del rodal (n = 30). Valor crítico = +/- 0,37

Parameter	Eigenvector 1	Eigenvector 2
Altitude	-0.01	-0.33
Topographic position	0.52	0.38
Exposure	0.29	-0.01
Slope aspect	-0.43	-0.26
Slope angle	-0.42	0.01
Soil depth	-0.55	-0.44
Drainage	-0.82	-0.27
% sand	0.29	-0.15
% silt	-0.28	0.21
% clay	-0.26	0.04
% organic matter	-0.56	-0.14
Total N	-0.72	-0.13
C: N	0.44	0.06
Extractable P	0.02	0.18
" " K	-0.26	0.00
" " Mg	-0.36	0.20
" " Ca	0.25	-0.21
pH	-0.08	0.01
Minimum stand age	-0.32	-0.17

DCA axis 2 did not correlate as strongly
as axis 1 with any one of the measured site
parameters (Table 2), but circumstantial
evidence suggests that local climatic varia-
tion (e.g. in minimum temperatures) could be
involved. High-scoring plots tended to be
located in the interior of the range, where
cold air ponding is likely. Low-scoring plots
tended to be close to the margin of the sum-
mit plateau, where there are fewer topo-
graphic barriers to downslope cold air drain-
age. Several of the low-scoring species on
axis 2 (e.g. *Myrceugenia chrysocarpa*,
Amomyrtus luma, *Podocarpus nubigena*) are
strongly associated with maritime climates,
which is consistent with a possible sorting on
axis 2 by minimum temperatures. However,
given the lack of quantitative evidence, and
the relatively low proportion of the total
variance explained by this axis, its interpreta-
tion was not pursued in depth.

*Distribution of stand ages, and
disturbance history*

Minimum stand age ranged from 130 to c.
770 years, although stands > 400 yrs old

were scarce (Fig. 3). 40% of all stands (17/
43) were between 275 and 324 years old,
suggesting that much of the study area was
affected by coarse-scale disturbance around
300 years ago.

Minimum stand age was not significantly
correlated with soil total nitrogen, which was
used as an index of site fertility (r = 0.159),
or with topographic position (r = -0.133). As
these analyses were applied only to stands >
200 years old, results suggest that stand-
initiating events in the centuries preceding
Hispanic settlement occurred at broadly si-
milar frequencies on sites of differing topo-
graphic position and soil fertility.

DISCUSSION

Determinants of stand composition

Variation in the species composition of
mature stands in the summit plateau forests
of the Cordillera Pelada is associated pri-
marily with gradients of soil fertility and
drainage, which in turn are at least partially
controlled by topography.

In humid temperate mountainous regions
throughout the world, soil depth and fertility
generally increase along topographic
gradients from ridgetop to gully (Jenny
1980), and vegetation studies show parallel
compositional gradients (e.g. Whittaker
1956, Gagnon & Bradfield 1987, Burns &
Leathwick 1996). Edaphic and compositional
gradients are rather weakly linked to topo-
graphy on the summit plateau, as demonstrat-
ed by the stronger correlation of DCA axis 1
with soil drainage, N-content and depth than
with the topographic index (Table 2). This
probably reflects the influences of spatial
variation in parent material (mica-schists vs
quartzite) on soil development (Veblen &
Ashton 1982), resulting in considerable
variation of soil parameters within topo-
graphic classes.

The main compositional gradient also
showed a weaker correlation with slope
aspect, species associated with low soil
fertility tending to occur more frequently on
north-facing slopes. Perez et al. (1991)
described a similar pattern on the tops of the
coastal ranges further south, on Isla Grande
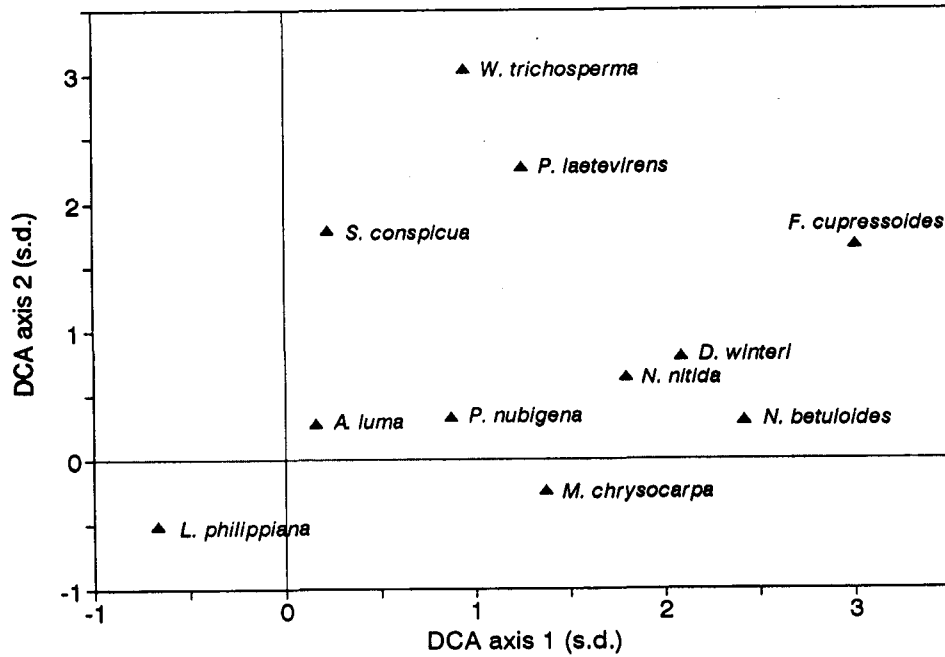de Chiloé. The effect of slope orientation on

Fig. 2: Species scores on first two DCA axes, Cordillera Pelada summit plateau, using data from stands 200-400 yrs old. Species are *Amomyrtus luma*, *Drimys winteri*, *Fitzroya cupressoides*, *Laureliopsis philippiana*, *Myrceugenia chrysocarpa*, *Nothofagus betuloides*, *Nothofagus nitida*, *Podocarpus nubigena*, *Pseudopanax laetevirens*, *Saxegothaea conspicua*, *Weinmannia trichosperma*.

Ordenamiento DCA de 11 especies arbóreas de las cimas de Cordillera Pelada, usando datos de rodales de 200-400 años de edad.
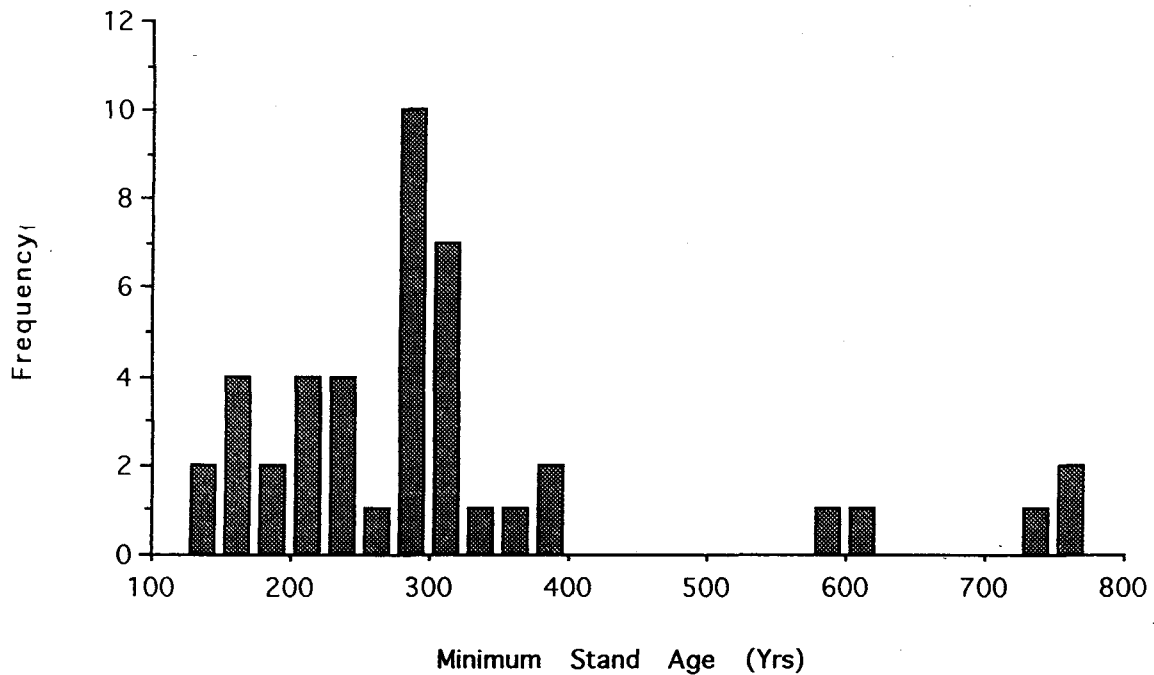

Fig. 3: Distribution of minimum stand ages for 43 sites on Cordillera Pelada summit plateau.

Distribución de edades mínimas para 43 rodales de las cimas de Cordillera Pelada.

site water balance and evapo-transpiration would be expected to have less bearing on plant survival and growth in the very humid climate of Cordillera Pelada than in the Mediterranean region of central Chile. However, aspect could operate in species sorting during extreme weather events such as droughts, or through effects on soil development (Allen & Peet 1990).

There was little evidence of variation in stand age in relation to major environmental gradients, suggesting *prima facie* that spatial variation in disturbance frequency was not important in determining the vegetation mosaic. However, there was some evidence of variation in the dominant *agents* of disturbance in relation to site quality. During soil sampling, charcoal fragments were found in the mineral soil beneath three *Fitzroya cupressoides* stands on low fertility sites, and also on one intermediate fertility site dominated by *Weinmannia trichosperma, Nothofagus nitida* and *Saxegothaea conspicua*. All four of these stands belonged to the modal age class (275-300 years old). In contrast, no charcoal was found on high fertility sites. Although the possibility of poorer charcoal preservation on the fertile sites (due to better drainage and greater biological activity in the soil) cannot be ruled out, there is therefore some evidence for higher fire frequency on the low fertility sites. This may be related to the frequent location of low fertility sites on upper slopes and plateaux, and also to the flammability of the dominant species (the conifer *F. cupressoides*) which is apparent from the destructiveness of 19th and 20th century human-set fires (Veblen & Ashton 1982).

In contrast, stand blowdown is likely to be more frequent on the higher fertility sites, as the tallest-growing species there (*N. nitida*) is much more susceptible to damage or snapping by storms than the very windfirm *F. cupressoides*. Three even-aged stands on high fertility sites, and two on sites of moderate fertility, showed strong evidence of a blow-down origin, in that most of the *N. nitida* trees appeared to have established on fallen logs and other elevated microsites (see also Lusk, 1996). No such evidence of stand turnover by blowdown was discernible in *Fitzroya* stands on low fertility sites.

The relative frequencies of fire and blow-down therefore probably do vary in relation to site quality in the study area, and this is of interest in that these two disturbance agents may have different consequences for vegetation dynamics (see Veblen et al. 1989). However, any spatial variation in disturbance regimes that does occur on the summit plateau seems likely to be at least partially controlled by inherent characteristics of the vegetation itself (differences in flammability and windfirmness), which in turn is determined mainly by site quality (Table 2) - consistent with the conclusion that soil drainage, N-content and depth are the key controls on vegetation composition.

Species' site requirements

According to Binkley & Vitousek (1989), although soil total nitrogen is often a poor index of nitrogen availability over small gradients and where recent site disturbance is important, it is likely to be a good indicator for comparisons of undisturbed stands across a large N gradient, as is the case in the present study. Species' scores on DCA axis 1 therefore provide a basis for broad comparisons of their relative nitrogen requirements.

In a nutrient gradient experiment with seedlings of nine tree species of the coast range forests, *Laureliopsis philippiana* showed higher tissue nitrogen content than any other species, and low nutrient availability impaired growth of *L. philippiana* more than that of any of its associates (Lusk et al. in press). This result is consistent with *L. philippiana*'s position at the upper end of the fertility gradient associated with DCA axis 1, suggesting that it is the most nitrogen-demanding of the 11 species. On the other hand, the association of *Fitzroya cupressoides* and *Nothofagus betuloides* with the poorest soils of the study area is in agreement with other studies which have reported these species growing on shallow, poorly-drained and/or low-nitrogen soils. *N. betuloides* is one of the first woody plants to establish on recent glacial moraines in Patagonia (Armesto et al. 1992), and both species are frequent colonizers of lava flows and tephra deposits in the Andes of south-central Chile (Lara 1991).

However, the relatively low score of *Weinmannia trichosperma* on axis 1 requires some clarification. DCA scores reflect the centre of each species' distribution on the gradient, as determined by relative abundances of stems ≥ 10 cm dbh. While most species presented more-or-less Gaussian abundance responses to the site quality gradient, *W. trichosperma* had a highly skewed response, attaining greatest abundance near the more fertile end of its range on this gradient. This resulted in a fairly low score on DCA axis 1. Yet, in contrast to *L. philippiana* and *Amomyrtus luma*, *W. trichosperma* was frequently present as a minor component of *Fitzroya*-dominated stands on very infertile sites. Thus, despite its moderate score on DCA axis 1, *W. trichosperma* is clearly physiologically tolerant of infertile, poorly-drained soils.

Disturbance history on the coastal range summits

In the contrast to the seismically- and volcanically-active Andes, the Chilean coastal ranges have been considered to be infrequently affected by coarse-scale disturbance (Veblen et al. 1981, Armesto & Fuentes 1988). Several studies have indicated that fine-scale gap processes predominate in the low- to mid-altitude forests of the coastal ranges, with a consequent dominance by shade-tolerant tree species (Veblen et al. 1981, Armesto & Fuentes 1988, Lusk, 1996). However, evidence produced in this paper shows that pre-Hispanic disturbance regimes on the summit plateau of the coastal ranges may have differed markedly from those prevailing at lower elevations. The abundance of even-aged stands ca. 300 years old, and evidence for stand blowdown on several sites, indicates that stand-destroying disturbances may have been frequent on the summit plateau.

Charcoal found beneath *Fitzroya cupressoides* stands c. 300 yrs old suggests that fire may have been an important cause of stand disturbance even before European settlement and exploitation of the range summits. Armesto et al. (1995) speculated on a similar role of fire in the dynamics of *F. cupressoides* forests on the coast range summits further south, on Isla Grande de Chiloé,

despite the established belief that fires of non-anthropogenic origin have not been a major evolutionary or ecological influence on Chilean vegetation (Rundel 1981), due to the low frequency of electrical storms.

In looking for the causes of fire in the Cordillera Pelada during the 17th century, three possibilities must be considered: (1) natural ignition, (2) Mapuche Indians, and (3) colonists based at the nearby town of Valdivia, an isolated Spanish fortified outpost within the Mapuche-controlled south of Chile during this period. The latter option seems the least likely, as there was apparently minimal Spanish penetration of the hinterland around Valdivia before ca. 1750 (Guarda 1973). Furthermore, Lara & Aravena (unpublished) have found dendrochronological evidence of recurrent fires during the last millenium on the Cordillera Pelada summits, establishing an important pre-Hispanic role for fire in the dynamics of *F. cupressoides* forest on the coast range. The Mapuche used fire as a weapon in wartime (Encina 1954). They also practised a system of shifting cultivation, and are believed to have used fire both to open up land for cultivation and to destroy their dwellings before moving on to establish new settlements (Dillehay 1990). The Cordillera Pelada summits seem highly unlikely sites for Mapuche settlement and cultivation during this period, in view of the much more favourable climates and soils to be found at lower altitudes in the central valley of southern Chile. However, at present there appears to be no evidence that would permit a distinction between natural and Mapuche-lit fires in this area.

The occurrence of extensive fires in such a wet climate seems surprising, but is rendered more comprehensible by a consideration of the significant Mediterranean influence that brings summer drought as far south as latitude 42° in Chile. Interpolations of rainfall maps in Almeya & Saez (1958) indicate that on average less than 10% of total annual precipitation on the range summits falls during the summer months of December to February. The widespread forest destruction and damage caused by 19th and 20th century human-set fires on the range summits leaves no doubt that these forests will burn during summer if a source of ignition is available.

Even-aged stands were also present in other forest types on more fertile sites. Several of these showed evidence of origin by blow-down (Lusk 1996), indicating that wind may also be an important agent of stand replacement on the coastal range summits, especially in *Nothofagus nitida*-dominant forests. The importance of wind disturbances in the dynamics of *Nothofagus* forests in other southern temperate regions has been well-documented (e.g. Wardle 1984).

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