# Composition and structure of remnant *Fitzroya cupressoides* forests of Southern Chile's Central Depression[1]

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FRAVER S., M. E. GONZÁLEZ, F. SILLA, A. LARA (Instituto de Silvicultura, Universidad Austral de Chile, Casilla 567, Valdivia, Chile), AND M. GARDNER (Conifer Conservation Programme, Royal Botanic Garden, Edinburgh, EH3 5LR U.K.) Composition and structure of remnant *Fitzroya cupressoides* forests of Southern Chile's Central Depression. J. Torrey Bot. Soc. 126:49–57. 1999.—Recently, several populations of *Fitzroya cupressoides* (Mol.) Johnst. (a rare conifer endemic to southern Chile and parts of adjacent Argentina) have been found in Chile's Central Depression, where it was thought to have been extirpated due to over-exploitation. Five of these populations exist as small forests (core areas ≤ 3 ha), where *Fitzroya* forms nearly pure stands. We established permanent plots in each of these five stands, determining tree ages and recording species composition. Multivariate analyses performed on both understory and tree species composition separated one stand from the remaining four, the differences being a function of stand ages and disturbance histories. Given their small size and isolation (from each other and from *Fitzroya* populations of the Coastal and Andean Cordilleras), these stands represent an extreme example of habitat fragmentation. A combination of conservation efforts is being undertaken to ensure their persistence in the Central Depression.

Key words: *Fitzroya cupressoides*, alerce.

*Fitzroya cupressoides* (Mol.) Johnst. (common name "alerce") is a rare, long-lived conifer endemic to the temperate rainforests of southern Chile and portions of adjacent Argentina. *Fitzroya* is a monotypic genus of the family Cupressaceae. Individuals can attain a size of over 4 m in diameter and 50 m in height, and can live longer than 3,600 years (Lara and Villalba, 1993), making *Fitzroya* one of the longest-lived tree species worldwide. Highly valued for its beautiful and durable wood, it was over-exploited for more than three centuries, which significantly reduced its original abundance. *Fitzroya*'s low competitive ability combined with the cattle grazing and repeated fires so common on harvested sites has greatly slowed or impeded its re-establishment in much of its natural habitat. Due to its scarcity and conservation threats, *Fitzroya* was listed in Appendix I of the Convention on International Trade in Endangered Species (CITES) treaty in 1975, in 1977, the Chilean government declared every living *Fitzroya* a "national monument," making its harvesting illegal. However, in spite of its legal protection, illegal harvesting still occurs (Veblen and Ashton 1982; Lara et al. 1996). Descriptions, in various levels of detail, of *Fitzroya* forests in the Coastal and Andean Cordilleras of southern Chile can be found in Espinosa (1917), Ramírez and Riveros (1975), Veblen et al. (1976), Veblen and Ashton (1982), Donoso et al. (1990), Lara (1991), Donoso et al. (1993), and Parker and Donoso (1993).

Prior to European colonization, *Fitzroya* forests occurred, often as scattered stands, throughout the Coastal Cordillera, the Andean Cordillera, and the wide Central Depression (west and south of Lago Llanquihue) that separates the two Cordilleras. The Central Depression was especially hard hit by harvesting due to flat terrain, ease of access, and closeness to the shipping

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port of Puerto Montt. Just north of Puerto Montt, an extensive *Fitzroya* forest may have covered 7,500 hectares of the Central Depression (Donoso 1994). This area was visited by Reiche (1934), who reported that although the former extensive *Fitzroya* forests had been destroyed, several forested areas remained perfectly conserved. From the same area, Heusser (1966) mentioned *Fitzroya* growing on the margins of a bog in which he collected palynological samples. However, by the time *Fitzroya* received legal protection (mid 1970's), it was thought to have been extirpated in the Central Depression. Golte (1996) reported that, "All that remains today of the once extensive[*Fitzroya* forests]in the southern longitudinal depression are the dead stumps."

However, in 1989, the Chilean Forest Service (CONAF) located a remnant stand of *Fitzroya* in the Central Depression. Over the past two years, additional sites that support living *Fitzroya*s have been located in the Central Depression. Currently, 13 sites are known; five consist of small forest stands, and eight support scattered small trees and saplings.

The purpose of this study was to describe the composition and structure of these remnant *Fitzroya* forests of the Central Depression. Due to the scarcity of this forest type and the fact that it was only recently discovered, it has not been previously described in any detail. This current study is an early step toward the eventual goal of restoring these Central-Depression *Fitzroya* forests.

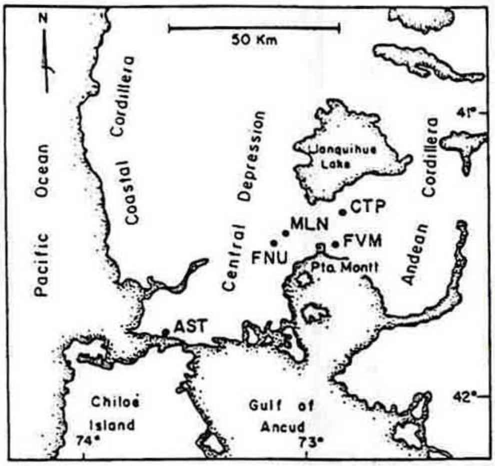


Fig. 1. Location of the five *Fitzroya cupressoides* study sites in southern Chile.

**Methods.** STUDY SITES. As stated above, five of the 13 currently-known *Fitzroya* stands in the Central Depression are small forests, scattered throughout the Central Depression (Fig. 1). Study plots were established on each of these five stands, which are locally referred to as (our codes given in parentheses): Astillero (AST), Colonia Tres Puentes (CTP), Fundo Nuñez (FNU), Fundo Von Meyer (FVM), and Monumento Natural Lahuén Ñadi (MLN).

These stands consist of core areas in which the overstory species composition is almost exclusively *Fitzroya*. The core areas, which range in size from less than one hectare to three hectares, are surrounded by scattered *Fitzroya* individuals. Elevations range from 35 to 175 m above sea level. All stands have experienced some degree of anthropogenic alteration, either from selective timber harvesting, cattle grazing, or fire. Four of the stands are privately owned; stand MLN is state owned and administered by CONAF.

All five stands occur on acidic, shallow, poorly-drained soils referred to as *ñadis*, which originated from Holocene volcanic ash deposited over fluvioglacial sediments. Upper horizons typically have a pH of 5.0 (Besoain 1985). At the lower limit of the B horizon (0.4 to 1 m below the soil surface) there is a 5- to 10-mm-thick hardpan formed by iron and magnesium oxides (Grez and Carmona 1982). This hardpan limits root development and greatly impedes drainage; these stands often have pools of standing water during the winter months, yet can be very dry during the summer. The C horizon consists of fluvioglacial sediments of sand and gravel. *Ñadis* are classified as Gleysols (FAO-UNESCO 1971).

The nearest weather station in Puerto Montt registers a mean annual temperature of 11.5 °C and an annual rainfall of 1912 mm, with the winter months (June–August) receiving the most rain.

DATA COLLECTION AND ANALYSIS. On each of the five stands, one 20 × 24-m permanent study plot was established. Given the small size of these forests and the complications caused by forest edge effects, a plot of this size was near the largest that could have been used in order to adequately describe the forest interiors. The locations of initial plot corners were chosen randomly (although within the limits dictated by the small size of the stands) using a random numbers table and a grid with 1 × 1-m divisions. To facilitate data collection, each plot was divided into four 10 × 12-m subplots, and each subplot contained two 3.16 × 3.16-m modules (10 $m^2$) placed in opposing corners. These modules were used to estimate vegetation parameters for each subplot. This sampling design is an adaptation of standard methods developed by Peet et al. (1996) for use in forests of the eastern United States.

Percent cover (in one of ten classes) was estimated and recorded for each vascular plant species in the 10-$m^2$ modules. The entire subplot was then searched for any species not encountered in the module, and percent cover was recorded for each of these species. Frequency for each species was determined as the percentage of subplots per plot that contained that species. In each subplot, tree diameter at breast height (dbh) was recorded by species for trees over 5 cm dbh. To determine tree ages and growth rates, we extracted increment cores from all trees at 0.3 m above ground level and at 0.6 m when tree centers were rotten. The cores were mounted, sanded, and processed using the standard tree-ring methods of Stokes and Smiley (1968).

For non-tree species (shrubs, lianas, hemiparasites, ferns, and herbs), tree seedlings (individuals < 2 m in height), and tree saplings (individuals < 5 cm dbh and ≥ 2 m in height), importance values (Greig-Smith 1983; Brower and Zar 1984) were calculated as the sum of mean relative cover and relative frequency per plot. Collectively, these categories are referred to as understory. Importance values for adult tree species were calculated as the sum of mean relative basal area, relative frequency, and mean relative density. All importance values within the understory and tree strata were relativized so that values had a possible range between 0 and 100. Data were collected in April (near the end of the growing season), 1997.

To examine the similarities in understory and tree species composition among the five stands, we used cluster analyses based on species importance values, with the Czekanowski index as the distance measure, and group-average as the linkage method (Pielou, 1984). Both cluster analyses ultimately produced highly-chained dendrograms, where the addition of groups, one at a time, to an already-formed larger group does not produce recognizable subgroups (Pielou 1984; McCune and Medford 1995). For this reason, the similarities were further investigated by two-way indicator species analyses (TWINSPAN, Hill 1979), a classification technique that assigns samples to groups based compositional similarity. All analyses were carried out using PC-ORD software, version 2.0 (McCune and Medford 1995).

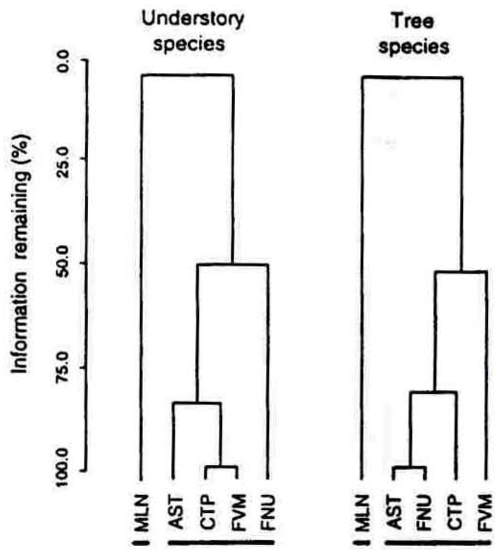


Fig. 2. Dendrograms based on importance values of understory and tree species. TWINSPAN groupings are indicated by bold lines under stand codes. Both the dendrograms and the TWINSPAN results indicate that stand MLN (the oldest, least disturbed stand) is distinct from the remaining (younger, more recently disturbed) stands.

**Results and Discussion.** A total of 16 tree species (including those found as seedlings or saplings) and 52 understory taxa (all non-arboreal vascular plants) were found on the five stands. Forty-five of the understory taxa were identified to the species level, six to the genus level, and one to the family level. A list of these taxa with their importance values can be found in the Appendix.

The canopies of all stands were clearly dominated by *Fitzroya*, giving one the impression of a pure stand. The results of the cluster analyses showed that, for both understory and tree strata, the species composition of stand MLN (the oldest and least disturbed) appears to be distinct from the remaining stands (Fig. 2). However, both dendrograms were highly chained (100 %), suggesting caution in their interpretation. TWINSPAN results also indicated that stand MLN was distinct from the others (Fig. 2). Neither the cluster analyses (based on percent chaining) nor TWINSPAN detected sub-groups among the four younger stands. Thus, the corroboration of the two methods suggests that the MLN stand is indeed distinct from the remaining stands, in terms of understory and tree species composition, and that no dramatic differences in species composition exist among the remaining stands. The differences between stand MLN and the others appear to be a function of its development: the closed canopy allows little light to enter the subcanopy and understory layers, thereby influencing species composition.

Aside from the presence of several cut stumps of *Fitzroya*, stand MLN had no apparent signs of disturbance. Stand AST had experienced selective logging at some point in the past. Stand CTP had experienced selective logging and possibly fires in the early 1960's (José Camilo Gómez, the owner, pers. comm.). In addition, cattle occasionally graze within this forest. Likewise, stand FVM had experienced selective logging, which had removed a significant amount of *Fitzroya* basal area, as evidenced by large cut stumps. Finally, stand FNU had experienced cattle grazing as well as a low-intensity fire that occurred in the early 1940's (Alfredo Nuñez, the owner, pers. comm.; fire damage evident in 1943 aerial photographs; and fire scars present on *Fitzroya* trunks). The fire was not intense enough to kill adult trees, yet it apparently opened the stand enough to cause a wave of *Fitzroya* regeneration. Ages of smaller *Fitzroya* trees from this stand dated to 50 years, providing evidence of their post-fire establishment.

Thus, stand MLN is the only known example of an older-growth *Fitzroya* forest in the Central Depression. Using its composition as representative of such forests, one might describe this forest type as being a nearly pure stand of *Fitzroya* (representing 94% of the total basal area) with the *Crinodendron hookerianum* and *Caldcluvia paniculata* abundant in the sub-canopy. Seedlings and saplings of *Amomyrtus* spp. and *Crinodendron hookerianum* are common. The understory consists primarily of the shrubs *Myrceugenia parviflora*, *Pernettya insana*, and *Philesia magellanica;* the lianas *Griselinia racemosa* and *Mitraria coccinea;* filmy ferns of the genus *Hymenophyllum*; the bamboo *Chusquea macrostachya;* and the creeping herb *Nertera granadensis*. Although not included in the analyses, mosses such as *Sphagnum* spp. and *Weinmoutia billardierii* are abundant: they typically occurr as scattered patches in the more poorly drained microsites.

In the younger stands, *Fitzroya* accounts for 78% of stand basal area (AST, CTP, FVM, and FNU pooled). *Drimys winteri* is much more abundant as a sub-canopy tree; in fact, at the FVM stand it exceeds *Fitzroya* in density (but not basal area or frequency). Seedlings and saplings of *Amomyrtus luma*, *Nothofagus nitida*, and *D. winteri* are abundant. The understory consists primarily of the shrubs *Pernettya insana*, *Philesia magellanica*, and *Gaultheria phillyreifolia;* the lianas *Griselinia racemosa*, *Luzuriaga radicans*, and *Campsidium valdivianum;* the ferns *Hymenophyllum* spp. and *Blechnum chilense;* and the sedge *Uncinia erinacea*.

Due to the variety of site conditions and elevations at which *Fitzroya* forests are found, their structure and composition vary considerably throughout *Fitzroya*'s range. For this reason, the forests described here do not correspond well with any published descriptions of *Fitzroya* forests of the Coastal Cordillera (see Ramírez and Riveros 1975; Veblen and Ashton 1982; Donoso et al. 1990; Parker and Donoso 1993), nor the Andean Cordillera (see Donoso et al. 1990, Lara 1991, Parker and Donoso 1993). Considering both basal area and understory species composition, they most closely resemble a forest described by Donoso et al. (1990) as a *Fitzroya–Nothofagus nitida* forest subtype that exists on poorly drained, thin volcanic soils of the lower valleys of the Andes, between 600 and 800 m elevation. In this subtype, as well as in our Central Depression stands, *Fitzroya* accounts for the majority of the stand's basal area (77% and 85%, respectively, considering all our study stands together), followed by *N. nitida* (12% and 5%, respectively). More abundant on our stands is *Drimys winteri* (also representing 5% of stand basal area). Some of the more common understory species found in both forest types are *Chusquea macrostachya*, *Philesia magellanica*, *Myrceugenia parviflora*, and *Gaultheria phillyreifolia*. (based on frequencies published for Donoso et al.'s [1990] subtype and importance values from our stands).

The differences in species composition between the Central Depression *Fitzroya* stands and those of the Coastal and Andean Cordilleras are likely the result of lower rainfall and a longer growing season in the Depression. Due to the orographic effect on rainfall, the western slopes and summits of both Cordilleras receive annual precipitation from 3000 to 5000 mm (Almeyda and Saez 1958; Armesto et al. 1996; Veblen et al. 1996). However, the Central Depression lies

Table 1. General stand information, as well as basal areas (BA), age ranges, and seedling and sapling densities for *Fitzroya cupressoides* in each stand. Stand area represents the approximate size of the forest core, that area where the canopy consists almost exclusively of *Fitzroya*.

| Stand | Stand code | Stand area (ha) | Species richness (per plot) | Canopy cover (%) | *Fitzroya cupressoides* BA (sq. m/ha) | Age range (years) | Seedlings (per ha) | Saplings (per ha) |
|---|---|---|---|---|---|---|---|---|
| Fundo Nuñez | FNU | 1 | 46 | 34.0 | 18.1 | 29–108 | 25604 | 14250 |
| Fundo Von Meyer | FVM | 0.8 | 41 | 36.3 | 28.9 | 135–235 | 1063 | 500 |
| Colonia Tres Puentes | CTP | 2 | 36 | 71.5 | 44.4 | 72–114 | 563 | 271 |
| Astillero | AST | 3 | 36 | 74.0 | 74.0 | 117–230 | 438 | 21 |
| Mon. Lahuén Ñadi | MLN | 2.5 | 33 | 94.6 | 154.5 | 198–316 | 0 | 0 |

in the Coastal Cordillera's rainshadow, where annual precipitation diminishes to 1912 mm (registered at the Puerto Montt station). Based on the available information on soil properties of *Fitzroya* forests, the Central-Depression sites do not appear to differ in any consistent way from those of the Cordilleras. Besoain (1985) reports a pH of 5.0 for the Central Depression *ñadi* soils; similar values have been reported from the *Fitzroya* forests of the Coastal (Donoso 1981; Pérez 1996) and the Andean Cordillera (Veblen et al. 1976; Peralta et al. 1979 [cited in Veblen et al. 1995]). Soils of *Fitzroya* forests of the three physiographic regions are thin: 40 to 100 cm in the Central Depression (Grez and Carmona 1982), 20 to 80 cm in the Andean Cordillera (Veblen et al. 1976), and 10 to 30 cm on the summits of the Coastal Cordillera (Veblen and Ashton 1982). The high variability in soil texture of *Fitzroya* sites within each Cordillera complicates any comparisons between physiographic regions, especially for the Andean Cordillera, where soil texture varies according to elevation and parent material, as well as distance from volcanic cones (Donoso 1994; Veblen et al. 1995).

Growth rates of *Fitzroya* are substantially higher in the Central Depression than in the two Cordilleras. Annual ring widths from various sites in the Coastal Cordillera range from 0.36 to 2.99 mm, and in the Andean Cordillera from 0.28 to 2.50 mm (Neira 1995, Lara, unpublished data). In the Central Depression we found ring widths from 0.78 to 5.70 mm. We assume the faster growth to be the result of the Central Depression's longer growing season.

The relationship between stand development and various site descriptors can be seen in Table 1, where stands are arranged from lesser to greater basal area, a measure of their development. As a stand develops (reflected in increased basal area) the canopy cover increases and the density of seedlings and saplings drops off dramatically (due to *Fitzroya's* shade intolerance). In addition, species richness decreases, presumably due to the presence of exotic species or agricultural weeds (such as *Cotula scariosa*, *Crepis* sp., *Plantago truncata*, *Poa annua*, and *Prunella vulgaris*) on the more open, younger stands.

The relationship between disturbance and *Fitzroya* regeneration in these stands is addressed only briefly here; a more detailed discussion can be found in Silla et al. (in review). All stands show narrow age ranges of adult trees (Table 1), which suggests a single wave of establishment, and a subsequent drop-off in recruitment (due to *Fitzroya*'s shade intolerance) as the canopy closes. Such single-cohort populations have been found in *Fitzroya* forests of the Coastal and Andean Cordilleras (Veblen and Ashton 1982; Donoso et al. 1990; Lara 1991; Donoso et al. 1993). The scarcity of *Fitzroya* recruitment on stands with closed canopies (generally older stands) suggests that, in the absence of canopy-opening disturbance, these stands are not self-replacing. That is, the current *Fitzroya* cohort may simply continue to age, with no further recruitment taking place. However, due to *Fitzroya's* longevity, it can maintain dominance for many centuries, during which time additional sites may become available for establishment (Lara 1991).

The age of the oldest tree in these stands (316 yrs, stand MLN) is a small fraction of *Fitzroya's* potential life span (over 3,600 yrs in the Andes; Lara and Villalba, 1993). The longevity of *Fitzroya* trees makes difficult any prediction concerning changes in plant species composition over time, and unfortunately no true old-growth *Fitzroya* forests remain in the Central Depression to serve as reference stands. In addition, it is not known if the maximum ages attainable for *Fitzroya* in the Central Depression are comparable to those of the Andes. Aside from the current study, the only tree ages available from the Central Depression were obtained near the MLN stand from six cut *Fitzroya* stumps, which had tree-ring counts between 465 and 712 years at time of cutting (Lara and Wolodarsky, unpubl. data).

Based on evidence from stand FNU and several of the very young *Fitzroya* populations in the Central Depression surveyed by Silla (1997), it appears that *Fitzroya* can colonize sites opened up by fires. This finding is consistent with that of Veblen and Ashton (1982) who reported abundant regeneration following low-intensity fires in the Coastal Cordillera. Thus, the current *Fitzroya* populations found in the Central Depression may have become established following fires that patchily affected the Depression, creating appropriate colonization sites. The stands may have originated from seed input from neighboring sites or from sucker sprouts, as *Fitzroya* is known to reproduce vegetatively (Veblen and Ashton 1982; Lara 1991; Parker and Donoso 1993; Silla 1997).

**Conservation Status.** The Central Depression *Fitzroya* stands are small populations, many kilometers distant from one another, and set in a landscape with increasing urban and suburban pressure from the nearby cities of Puerto Montt and Puerto Varas. The small sizes and isolation of the stands from each other and from *Fitzroya* populations of the Coastal and Andean Cordilleras represent an extreme case of habitat fragmentation. If edge effects (altered species composition, community structure, and microclimate) extend anywhere near the 137 m found in conifer forests of the Pacific Northwestern United States (Chen et al. 1992), no true forest interior exists in the *Fitzroya* forests of the Central Depression. The effect of this fragmentation on the species composition, stand dynamics, and persistence of associated species is unknown, as no large, continuous old-growth forests remain in the Central Depression for comparative studies. Despite the possible problems related to their size and location, the stands are nonetheless important because they represent reproductive populations in an area where *Fitzroya* was thought to have been extirpated.

Fortunately, the recent public and scientific interest in these stands has stimulated landowner interest in their protection. In addition, we have initiated a restoration program, in which nursery-grown *Fitzroya*, successfully produced from both seeds and cuttings, will be planted on several sites in the Central Depression. (The results of this study will aid in determining which other species, and in what proportions, should be planted.) Taking into account the possibility that *Fitzroya* populations of the Central Depression may represent a genotype distinct from those of the Coastal and Andean Cordilleras, seeds and cuttings are being collected only from sites in the Depression. The relatively rapid growth of this "slow-growing" species in the Central Depression, coupled with the fact that *Fitzroya* plants propagated from seed can attain a height of 1 m after three years in the nursery (B. Escobar, pers. comm.), suggest the possibility of rapid stand development on restoration sites.

Thus, a combination of conservation efforts—including legal habitat protection (as in stand MLN), voluntary protection (resulting from awareness of private landowners), and active restoration—is being used to increase the likelihood that *Fitzroya* will persist in the Central Depression.

## Literature Cited


ALMEYDA, A.E. AND S.F. SAEZ. 1958. Recopilación de datos climáticos de Chile y mapas sinópticos respectivos. Ministerio de Agricultura, Santiago.

ARMESTO, J.J., J.C. ARAVENA, C. VILLAGRAN, C. PEREZ, AND G.G. PARKER. 1996. Bosques templados de la Cordillera de la Costa, p. 199–212. *In* J.J. Armesto, C. Villagran, and M.K. Arroyo [eds.], Ecología de los Bosques nativos de Chile. Editorial Universitaria, Santiago.

BESOAIN, E. 1985. Los suelos, p. 25–106. *In* J. Tosso [ed.], Suelos Volcánicos de Chile, Chap. 1. Instituto de Investigaciones Agropecuarias, Ministerio de Agricultura, Santiago.

BROWER, J.E. AND J.H. ZAR. 1984. Field and Laboratory Methods for General Ecology. Wm. C. Brown Publishers. Dubuque, Iowa, USA. 226 p.

CHEN, J., J.F. FRANKLIN, AND T.A. SPIES. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications 2: 387–396.

DONOSO, C. 1981. Investigación y desarrollo forestal; tipos forestales de los bosques nativos de Chile. Documento de Trabajo No. 38. Corporación Nacional Forestal, Santiago. 82 p.

DONOSO, C. 1994. Bosques templados de Chile y Argentina: variación, estructura y dinámica. Editorial Universitaria, Santiago.

DONOSO, C., R. GREZ, AND V. SANDOVAL. 1990. Caracterización del tipo forestal alerce. Bosque 11(1): 21–34.

DONOSO, C., V. SANDOVAL, R. GREZ, AND J. RODRIGUEZ. 1993. Dynamics of *Fitzroya cupressoides* forests in southern Chile. Journal of Vegetation Science 4: 303–312.

ESPINOSA, M.R. 1917. Los alerzales de Piuchué. Boletín del Museo Nacional (Chile), tomo 10: 36–93.

FAO-UNESCO. 1971. Soil map of the world. South America, IV. Paris. 193 p. plus maps.

GOLTE, W. 1996. Exploitation and conservation of *Fitzroya cupressoides* in southern Chile. p. 123–150. *In* D. Hunt [ed.], Temperate Trees under Threat. International Dendrology Society.

GREIG-SMITH, P. 1983. Quantitative Plant Ecology. University of California Press, Berkeley, California, USA. 359 p.

GREZ, R. AND A. CARMONA. 1982. Utilización silvoagropecuaria de los terrenos de ñadi: caracterización de los suelos. Ciencias Forestales, Universidad Austral de Chile. Informe de Convenio. 24 p.

HEUSSER, C.J. 1966. Late-Pleistocene pollen diagrams from the Province of Llanquihue, southern Chile. Proceedings of the American Philosophical Society 110(4): 269–305.

HILL, M.O. 1979. TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics, Cornell University, Ithica, NY.

LARA, A. 1991. The dynamics and disturbance regimes of *Fitzroya cupressoides* forests in the south-central Andes of Chile. PhD thesis, Univ. of Colorado, Boulder.

LARA, A. AND R. VILLALBA. 1993. A 3620-year temperature record from *Fitzroya cupressoides* tree rings in southern South America. Science 260: 1104–1106.

LARA, A., C. DONOSO, AND J.C. ARAVENA. 1996. La conservación del bosque nativo de Chile; problemas y desafios. p. 335–362. *In* J.J. Armesto, C. Villagran, and M.K. Arroyo [eds.], Ecología de los Bosques Nativos de Chile. Editorial Universitaria, Santiago.

MCCUNE, B. AND M.J. MEDFORD. 1995. PC-ORD; Multivariate Analysis of Ecological Data, Version 2. Gleneden Beach, Oregon, USA.

NEIRA, E.P. 1995. Desarrollo de cronologías para alerce (*Fitzroya cupressoides*) en las Cordilleras de la Costa y de los Andes. Thesis, Univ. Austral de Chile, Valdivia.

PARKER, T. AND C. DONOSO. 1993. Natural regeneration of *Fitzroya cupressoides* in Chile and Argentina. Forest Ecology and Management 59: 63–85.

PERALTA, M., N. KLENNER, S. GONZALEZ, AND E. BESOAIN. 1979. Suelos forestales representativos de la Cordillera de los Andes; un transecto en el sector de Contao, Provincia de Chiloé, X Region. Facultad de Ciencias Forestales, Univ. de Chile, Santiago. Boletin Técnico 55.

PEREZ, C. 1996. Los procesos de descomposición de la materia orgánica en bosques templados costeros: interacción entre suelo, clima y vegetación, p. 301–315. *In* J.J. Armesto, C. Villagran, and M.K. Arroyo [eds.], Ecología de los Bosques Nativos de Chile. Editorial Universitaria, Santiago.

PEET, R.K., T.R. WENTWORTH, R. DUNCAN, AND P.S. WHITE. 1996. North Carolina Vegetation Survey protocol: a flexible, multipurpose method for recording vegetation composition and structure (version 2.0). University of North Carolina, Chapel Hill, USA.

PIELOU, E.C. 1984. The Interpretation of Ecological Data; a Primer on Classification and Ordination. John Wiley & Sons, New York. 263 p.

RAMIREZ, C. AND M. RIVEROS. 1975. Los alerzales de Cordillera Pelada: flora y fitosociología. Medio Ambiente 1(1): 3–13.

REICHE, K.F. 1934. Geografía Botánica de Chile. Imprenta Univesitaria, Santiago.

SILLA, F. 1997. Dinámica regenerativa del alerce (*Fitzroya cupressoides*) en la Depresión Intermedia. MS thesis, Univ. Austral de Chile, Valdivia.

SILLA, F., A. LARA, S. FRAVER, T. ALLNUTT, AND A. NEWTON. Regeneration dynamics of *Fitzroya cupressoides* in Chile's Central Depression. (In review).

STOKES, M.A. AND T.L. SMILEY. 1968. An Introduction to Tree-Ring Dating. Univ. of Chicago Press, USA. 73 p.

VEBLEN, T.T., R.J. DELMASTRO, AND J.E. SCHLATTER. 1976. The conservation of *Fitzroya cupressoides* and its environment in southern Chile. Environmental Conservation 3(4): 291–301.

VEBLEN, T.T., AND D.H. ASHTON. 1982. The regeneration status of *Fitzroya cupressoides* in the Cordillera Pelada, Chile. Biological Conservation 23: 141–161.

VEBLEN, T.T., B.R. BURNS, T. KITZBERGER, A. LARA, AND R. VILLALBA. 1995. The ecology of conifers of southern South America. p. 120–155. *In* N.J. Enright and R.S. Hill [eds.], Ecology of the Southern Conifers. Melbourne Univ. Press.

VEBLEN, T.T., T. KITZBERGER, B.R. BURNS, AND A.J. ROBERTUS. 1996. Perturbaciones y dinámica de regeneración en bosques andinos del sur de Chile y Argentina. p. 169–198. *In* J.J. Armesto, C. Villagran, and M.K. Arroyo [eds.], Ecología de los Bosques Nativos de Chile. Editorial Universitaria, Santiago.

**Appendix**

Importance values for all vascular plant species. Values were calculated separately for trees and understory (including seedlings and saplings) vegetation. Sites are arranged from left to right in the order of older to younger.

| | Sites | | | | |
|---|---|---|---|---|---|
| | MLN | AST | CTP | FVM | FNU |
| Tree species | | | | | |
| *Fitzroya cupressoides* (Mol.) Johnst. | 53.52 | 59.82 | 45.98 | 37.23 | 47.20 |
| *Crinodendron hookerianum* Mol. | 14.82 | — | — | — | — |
| *Caldcluvia paniculata* (Cav.) D. Don | 13.35 | — | — | — | — |
| *Tepualia stipularis* (Hook et Arn.) Griseb. | 4.78 | 12.76 | 10.78 | — | — |
| *Gevuina avellana* Mol. | 4.55 | — | 6.79 | — | — |
| *Nothofagus nitida* (Phil.) Reiche | 2.52 | 16.39 | 4.30 | 20.77 | 20.69 |
| *Lomatia ferruginea* (Cav.) R. Br. | 2.32 | — | 1.95 | — | — |
| *Amomyrtus meli* (Phil.) Legr. et Kaus. | 2.08 | — | — | — | — |
| *Drimys winteri* Forst. | 2.08 | 11.02 | 24.04 | 42.00 | 13.82 |
| *Weinmannia trichosperma* Cav. | — | — | 4.23 | — | 2.35 |
| *Eucryphia cordifolia* Cav. | — | — | 1.93 | — | — |
| *Nothofagus dombeyi* (Mirb.) Bl. | — | — | — | — | 7.54 |
| *Amomyrtus luma* (Mol.) Legr. et Kraus. | — | — | — | — | 4.74 |
| *Podocarpus nubigena* Lindl. | — | — | — | — | 3.65 |
| Seedlings and saplings | | | | | |
| *Amomyrtus luma* (Mol.) Legr. et Kraus. | 16.23 | 3.70 | 1.78 | 2.66 | 2.71 |
| *Crinodendron hookerianum* Mol. | 13.53 | 2.25 | 1.23 | 0.87 | 0.42 |
| *Amomyrtus meli* (Phil.) Legr. et Kaus. | 6.05 | — | — | — | — |
| *Laureliopsis philippiana* Loos. | 4.85 | — | — | — | — |
| *Caldcluvia paniculata* (Cav.) D. Don. | 4.66 | 1.17 | 1.40 | — | — |
| *Tepualia stipularis* (Hook et Arn.) Griseb. | 3.79 | — | 18.08 | 9.20 | — |
| *Podocarpus nubigena* Lindl. | 2.74 | 2.72 | 1.76 | 0.64 | 2.69 |
| *Gevuina avellana* Mol. | 2.62 | 2.23 | 1.68 | — | 0.42 |
| *Eucryphia cordifolia* Cav. | 2.51 | — | 1.85 | 1.91 | 1.26 |
| *Lomatia ferruginea* (Cav.) R. Br. | 2.47 | 0.56 | 1.79 | 1.30 | 0.57 |
| *Drimys winteri* Forst. | 2.38 | 6.23 | 2.01 | 2.12 | 5.36 |
| *Weinmannia trichosperma* Cav. | 1.29 | 3.13 | 1.69 | 1.22 | 1.79 |
| *Fitzroya cupressoides* (Mol.) Johnst. | — | 2.50 | 2.53 | 2.58 | 26.25 |
| *Nothofagus nitida* (Phil.) Reiche | — | 2.24 | 4.15 | 7.22 | 6.71 |
| *N. dombeyi* (Mirb.) Bl. | — | — | — | 0.48 | 3.76 |
| *Saxegothaea conspicua* Lindl. | — | — | — | — | 0.42 |
| Shrub species | | | | | |
| *Myrceugenia parviflora* (DC.) Kaus. | 2.37 | — | 1.36 | — | 1.90 |
| *Pernyettya insana* (Mol.) Gunckel | 1.91 | 3.94 | 4.40 | 6.36 | 1.98 |
| *Philesia magellanica* Gmel. | 1.67 | 7.69 | 4.96 | 5.13 | — |
| *Pseudopanax laetevirens* (Gay) Harms. | 1.15 | 2.97 | 2.27 | 1.70 | 1.79 |
| *Gaultheria phillyreifolia* Poepp. et Endl. | 0.56 | 3.12 | 2.88 | 2.10 | 3.90 |
| *Desfontainia spinosa* Ruiz et Pav. | — | 2.21 | 1.34 | — | — |
| *Ugni molinae* Turcz. | — | — | 1.76 | 5.63 | — |
| *Myrteola nummularia* (Poir.) Berg. | — | — | 1.13 | 1.85 | 2.16 |
| *Pernettya angustifolia* (Lindl.) Reiche | — | — | — | 1.28 | 2.07 |
| *Gaultheria caespitosa* Poepp. et Endl. | — | — | — | 0.93 | 1.73 |
| *Baccharis* sp. | — | — | — | 0.43 | — |
| Lianas | | | | | |
| *Griselinia racemosa* (Phil.) Taub. | 2.47 | 9.06 | 7.63 | 10.56 | 1.01 |
| *Mitraria coccinea* Cav. | 2.44 | 2.58 | 1.91 | 1.70 | 1.78 |
| *Luzuriaga polyphylla* (Hook.) Mcbr. | 1.79 | — | — | — | — |
| *Campsidium valdivianum* (Phil.) Skottsb. | 0.65 | 3.45 | 2.81 | 2.37 | 4.17 |
| *Elytropus chilensis* (Muell.) Arg. | 0.56 | — | — | — | — |
| *Luzuriaga radicans* Ruiz et Pav. | — | 7.01 | 2.01 | 1.78 | 1.82 |
| Hemiparasites | | | | | |
| *Tristerix corimbosus* (L.) Kuijt | — | — | 0.96 | — | 1.38 |
| Ferns | | | | | |
| *Hymenophyllum pectinatum* Cav. | 2.88 | 3.07 | 2.97 | 2.56 | 0.84 |
| *Hymenoglossum cruentum* (Cav.) Presl. | 2.37 | 4.73 | 1.63 | 0.93 | 0.42 |
| *Hymenophyllum plicatum* Kaulf. | 2.18 | 0.52 | 1.32 | 1.76 | 1.62 |

**Appendix**
**Continued.**

| | Sites | | | | |
|---|---|---|---|---|---|
| | MLN | AST | CTP | FVM | FNU |
| *H. dentatum* Cav. | 1.70 | 2.17 | 1.82 | 2.83 | 1.86 |
| *Blechnum magellanicum* (Desv.) Mett. | 1.15 | 1.85 | 2.19 | 3.75 | — |
| *Asplenium dareoides* Desv. | 1.10 | — | — | — | — |
| *Hymenophyllum caudicaulatum* (Presl.) C. Chr. | 1.09 | 1.85 | — | — | — |
| *H. dicranotrichum* (Presl.) Sadebeck | — | 2.58 | 1.67 | — | — |
| *Grammitis magellanica* Desv. | — | 1.09 | 1.36 | 0.85 | 0.84 |
| *Lophosoria quadripinnata* (Gmel.) C. Chr. | — | 1.07 | — | 0.96 | — |
| *Blechnum chilense* (Kaulf.) Mettenius | — | 0.68 | 2.38 | 2.12 | 2.23 |
| *Hymenophyllum krauseanum* Phil. | — | 0.52 | — | 0.73 | — |
| *H. cuneatum* Kunze | — | — | 1.33 | — | 1.68 |
| *Blechnum pennamarina* (Poir.) Kuhn | — | — | — | 1.28 | 1.69 |
| *Polypodium feuillei* Bert. | — | — | — | 0.64 | — |
| *Gleichenia* sp. | — | — | — | — | 0.42 |
| *Hymenophyllum* sp. | — | — | — | — | 0.42 |
| Herbaceous species | | | | | |
| *Chusquea macrostachya* Phil. | 6.38 | 3.21 | — | — | — |
| *Nertera granadensis* (Mutis ex L. f.) Drude | 2.47 | 3.40 | 1.32 | 1.30 | 0.66 |
| *Uncinia erinacea* (Cav.) Pers. | — | 3.96 | 6.23 | 1.30 | 1.80 |
| *Chloraea* sp. | — | 0.56 | — | — | — |
| *Carex fuscula* D'Urville Hc. | — | — | — | 4.04 | — |
| *Juncus lesueuri* Bolander | — | — | — | 1.66 | — |
| *Viola* sp. | — | — | — | 0.87 | — |
| *Graminea* sp. | — | — | — | 0.43 | — |
| *Chusquea uliginosa* Phil. | — | — | — | — | 1.98 |
| *Juncus procerus* C. Meyer | — | — | — | — | 1.62 |
| *Shoenus rhynchosporoides* (Steudel) Kuk. Hc. | — | — | — | — | 1.24 |
| *Plantago truncata* Cham. et Schlecht. | — | — | — | — | 0.57 |
| *Cotula scariosa* (Cass.) Franchet | — | — | — | — | 0.42 |
| *Poa annua* L. | — | — | — | — | 0.42 |
| *Prunella vulgaris* L. | — | — | — | — | 0.42 |
| *Crepis* sp. | — | — | — | — | 0.40 |
| *Eliocharis pachycarpa* Desv. | — | — | — | — | 0.40 |