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Vegetation composition, structure, and biomass of two unpolluted watersheds in the Cordillera de Piuchué, Chiloé Island, Chile

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Abstract

Research in pristine forests provides a necessary reference of energy and nutrient cycling in absence of anthropogenic influence. Therefore two unpolluted watersheds in the Cordillera de Piuchué of southern Chile (42 °30′ S) were chosen for detailed ecosystem analysis. The goals of this study were to quantify the distribution of the living biomass in the research watershed and to document topographic gradients in the vegetation. Across a small spatial gradient from ravine bottom to ridgetop (approximately 60 m in elevation and $<$ 300 m in length) in the Cordillera de Piuchué watersheds, there were significant shifts in vegetation composition, structure, and biomass. Based on sampling in 18, 100 m^2 plots, we identified three distinct community associations: a *Fitzroya* forest at the bottom of the watershed, a mid-slope *Pilgerodendron-Tepualia* transition zone, and a ridgetop moorland community. The *Fitzroya* forest was dominated by a cohort of approximately 400 year-old *Fitzroya cupressoides* trees. Both tree basal area (138 m^2/ha) and total live biomass (656 Mg ha^{-1}) reached a maximum in this vegetation type. The *Pilgerodendron-Tepualia* forest consisted of smaller, shorter, and younger trees with dominance shared by *Pilgerodendron uviferum, Tepualia stipularis*, and to a lesser extent, *F. cupressoides*. Basal area and biomass were half that of the *Fitzroya* forest (69.5 m^2 ha^{-1}; 350 Mg ha^{-1}) but tree density was 65% greater. The moorland can best be described as an open community of mosses and cushion plants that included low stature individuals of *P. uviferum*, *F. cupressoides*, and *T. stipularis*. The size and age structure of *F. cupressoides* in the bottomland forest suggest that the current cohort of adult trees was established following a catastrophic disturbance and that *F. cupressoides* is unable to regenerate under its own canopy. In contrast, the size structure of the tree populations in the *Pilgerodendron-Tepualia* zone indicates that all the constituent tree species, except *F. cupressoides*, are able to reproduce at least at some microsites in the understory. The watershed-level means for live biomass were 306 Mg ha^{-1} of aboveground tree biomass, 25 Mg ha^{-1} of large root biomass (diameter $\geq$ 1 cm), and 46 Mg ha^{-1} of small root biomass (diameter $<$ 1 cm).

Introduction

Our knowledge of energy and nutrient cycling in temperate forests is based largely on studies from ecosystems affected by the multiple and varied impacts of human activity (Bormann & Likens 1979; Johnson & Lindberg 1992). Research in pristine forests provides a necessary reference of ecosystem functioning in absence of anthropogenic influence. For example, Hedin et al. (1995) evaluated the generality of biogeochemical theories, theories developed exclusively in locations subject to air pollution, by measuring the losses of major nutrients from forested watersheds in an unpolluted area of southern Chile. An uncertainty in this approach is the extent to which these remote forests are comparable to other old-growth temperate forests (Alaback 1991).

To address this uncertainty, two small watersheds included in the Hedin et al. (1995) study were chosen for an intensive investigation of ecosystem processes. The sites were located in the Cordillera de Piuchué on Chiloé Island off the coast of southern Chile (Figure 1). The forests are dominated by two long-lived and endemic conifer trees in the *Cupressaceae* family – *Fitzroya cupressoides* (Molina) Johnston and *Pilgerodendron uviferum* (D. Don) Florin. A striking feature of the vegetation in these coastal mountains is the steep elevation gradient in plant composition and structure (Aravena 1991; Ruthsatz & Villagrán 1991; Lusk 1996; Armesto et al. 1996). At the bottom of the watersheds, *F. cupressoides* forms dense, nearly monospecific stands of stunted trees. Midslope forests have a more open canopy composed of mix of *P. uviferum*, *F. cupressoides*, and *Tepualia stipularis* (H. et A.) Griseb. (*Myrtaceae*). At the summits, prostrate individuals of the dominant woody plants are interspersed with sedges and cushion plants typical of the moorland vegetation of Patagonia.

Previous work in the Cordillera de Piuchué established that there is little net retention of externally added (i.e., atmospherically deposited) nutrients in these watersheds. However, the nitrogen cycle was more complex with dissolved organic forms of N accounting for most of the N export (Hedin et al. 1995). Pérez et al. (1998) reported N mineralization rates that were lower than many temperate forests in industrialized regions of North America. Zarin et al. (1998) suggested that production and decomposition of soil organic matter largely control the cycling of mineral nutrients in this montane conifer forest. Armesto et al. (1995) noted the extensive fine root development in these forests and speculated that it may result in the efficient uptake of nutrients from the forest floor. Together these results describe an ecosystem where organic matter dynamics supersedes atmosphere/soil interactions as the more important determinant of nutrient supplies.

The physiognomy of the vegetation in Cordillera de Piuchué watersheds presents challenges to conducting ecosystems studies and to interpreting their results. The heterogeneity in biotic structure must be accounted for when making watershed level estimates of ecosystem parameters. Furthermore both *F. cupressoides* and *P. uviferum* are restricted to special edaphic conditions (i.e., shallow, wet soils) in the coastal range and form forests distinct from the more widespread types of temperate rainforests found on the South American mainland (Armesto et al. 1995; Veblen et al. 1995). The goal of this study was to quantify the current distribution of the living biomass in the research watersheds. We focused on the woody plants since they are the predominant class of primary producers. To accurately estimate the biomass pools, we needed to first document the composition and structure of the vegetation. The biomass results are the foundation on which to build nutrient and energy budgets for this ecosystem. In addition, our detailed vegetation analysis provides the necessary context for valid comparisons with other temperate forests.

Methods

Study site

The research sites comprised two adjacent, small watersheds on the western slope of the Cordillera de Piuchué on the island of Chiloé, Chile (74° W 43° S, Figure 1). There is no history of timber extraction or agricultural clearing in these high-elevation forests (Armesto et al. 1995). Inputs of atmospheric pollutants to the site are negligible (Hedin et al. 1995). Little change has occurred in the major forest taxa during the past 7500 years (Villagrán 1990). Major species of canopy trees include the endemic and threatened conifers, *Fitzroya cupressoides* and *Pilgerodendron uviferum*, and two evergreen species of southern beech (*Fagaceae*), *Nothofagus nitida* (Phil.) Krass. and *Nothofagus betuloides* (Mirb.) Oerst. Other important woody species are the trees, *Drimys winteri* J. R. et G. Forster (*Winteraceae*), and *Podocarpus nubigena* Lindl. (*Podocarpaceae*), and the tall shrub, *Tepualia stipularis*. Epiphytes and vines are common especially in the less exposed sectors of the watersheds. The understory is dominated by the shrubs, *Philesia magellanica* J. F. Gemel. (*Philesiaceae*) and *Desfontainia spinosa* R. et P. (*Desfontainiaceae*) along with dense patches of low stature bamboo, *Chusquea* sp. Nomenclature follows Marticorena & Rodriguez (1995).

Elevation ranges from 650 m at the bottom of the watersheds to 710 m at the top of the watersheds. The research watersheds are 2.1 ha (CP-1) and 1.0 ha in area (CP-2, Figure 1); both have a northeast aspect. Slope averaged 19% but slope varied from a maximum

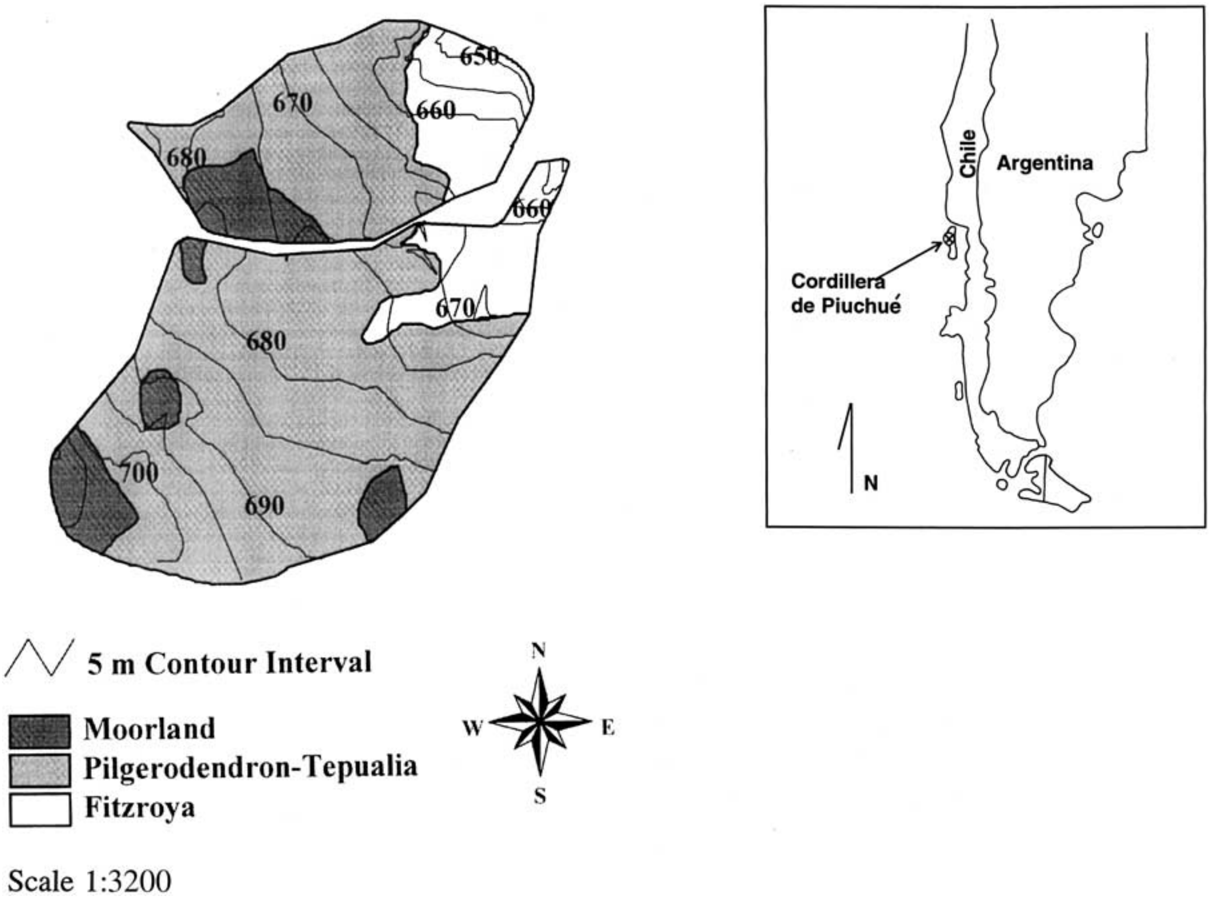

Figure 1. Topographic and vegetation map of the two research watersheds in the Cordillera de Piuchué. CP-1 watershed is the larger of the two watersheds and is located just south of the CP-2 watershed. Scale of the vegetation map 1:3200. Inset in the upper right shows the location of Chiloé Island in southern Chile.

of 74% at the stream outlet in CP-1 to a minimum of 6% at the most exposed ridgetop. Preliminary sampling was started in 1993, most plots were measured in 1994, and field work was completed in 1995. The climate of the region is a Pacific-coast maritime regime characterized by mild temperatures and high precipitation with average monthly precipitation greater than 10 cm even during the driest summer months (Alaback 1991). Prevailing westerly winds bring a nearly constant supply of moist air from the Pacific Ocean which is less than 15 km west of the site. There are no reliable records of temperature and precipitation for these coastal sites but based on existing information rainfall is between 400–500 cm yr^{-1} and mean annual temperature is approximately 6 °C. The geological foundation of the watersheds is Precambrian schist (Watters & Fleming 1962). Zarin et al., 1998, have tentatively classified the soils in the watersheds as Folists and Inceptisols; they are acidic (3.9–4.1 pH), shallow (generally 40 cm or less to bedrock), and occasionally water-saturated in areas of gentle slope.

Vegetation composition and structure

We surveyed 50×50 m grids across the watersheds. At each of 18 grid points that fell within the watersheds, we established an 10×10 m plot (100 m^2 ground area) to sample woody vegetation. For plots located in forest vegetation, we identified, tagged and measured the diameter at breast height (breast height = 1.37 m; dbh) of all standing trees (alive and dead) with a dbh $\geq$5 cm and all living woody saplings $\geq$ 2 m tall. For plots in the moorland vegetation, we identified and measured the basal stem diameter and height of all erect woody plants with a definable main stem and a basal diameter $\geq$5 cm. For prostrate clumps of woody vegetation, we identified the species and estimated the surface area covered by each clump by measuring the longest axis (major axis) and longest axis normal to the major axis. Aspect and slope angle were also noted for each plot.

Tree heights and ages

To quantify tree height distribution, we measured the total height and height to the base of the live crown for representative canopy trees in the forested plots. Canopy trees were individuals not subject to direct overhead shading. Our total sample of tree heights included 71 *F. cupressoides* trees, 43 *P. uviferum* trees, and 7 *Nothofagus nitida* trees. To measure the age structure of the *F. cupressoides* population, we collected increment cores from every individual > 10 cm dbh located in the vegetation plots on CP-2. Two radial cores were extracted from each tree; borings were taken at breast height. Cores were dried, mounted and sanded. Annual rings were identified and counted under a dissecting microscope to obtain ages for all stems following the procedures described in Stokes & Smiley (1968). To reduce the potentially large errors in age estimates that are associated with slow-growing, long-lived trees with extremely narrow rings (Villalba & Veblen 1997), we excluded ages interpolated from incomplete cores and built our age frequency distribution using data only from intact cores. Also note that since we took cores at breast height, our estimates are minimum ages since we did not include the time it took a stem to grow to breast height.

Aboveground woody biomass

We estimated the biomass of the live forest trees from species-specific and site-specific allometric equations. Given the pristine nature of the study site, destructive sampling of live plants for dimension analysis was used sparingly. For the protected *F. cupressoides*, we cut no live trees. Vann et al. (1998) describe their solution to these constraints and present dbh-to-biomass relationships for *F. cupressoides* and *P. uviferum*. Their method involved climbing the trees to measure the form of the stem, to record the number and basal diameter of branches, and to sample a limited number of live limbs. Bole mass was then calculated from stem volume and measures of wood density. Sampled branches were used to develop allometric equations predicting branch, twig, and foliage biomass from branch basal diameter. We used a similar approach to determine the allometric relationships for three other important tree species, namely *N. nitida, Drimys winteri*, and *Podocarpus nubigena* (C. Johnson 1999). In all cases, the adjusted R^2 values of the linear equation, log(mass) = constant + slope log(dbh), was > 0.97 and the p-values of the slope and constant were < 0.05.

The non-destructive techniques developed by Vann et al. (1998) could not be used to estimate the biomass of *Tepualia stipularis*, an abundant and morphologically plastic tall shrub. Therefore we measured the dbh and then destructively sampled 11 *T. stipularis* trees just outside of the research watersheds. The entire aboveground portion of the tree was weighed in the field and a subsample which included proportional amounts of stem, twig, and foliage was collected to estimate the wet-to-dry weight conversion.

F. cupressoides and *P. uviferum* trees tend to develop large, flared root crowns. This portion of the aboveground live biomass was not included in the allometric equations of Vann et al. (1998). To include this fraction, we estimated root crown mass as a linear function of dbh. We found seven dead *F. cupressoides* trees near the watersheds with exposed root crowns. These seven trees ranged from 9.1 cm dbh to 36.2 cm dbh. We measured all the dimensions necessary to estimate the volume of the root crown, cut-up and weighed at a least a quarter (by volume) of the crown, and collected a subsample for wet-to-dry weight conversion. This approximation of root crown mass was applied to both *F. cupressoides* and *P. uviferum* trees.

The six woody species for which we had allometric equations accounted for 96% of the tree basal area on the forest. *Nothofagus betuloides*, a species morphologically similar to *N. nitida*, contributed 2% of the total basal area. Therefore we used *N. nitida* biomass equations to estimate the biomass of *N. betuloides*. Using the criterion of morphological similarity, we made the following substitutions for the remaining tree species: *P. nubigena* equations for *Saxegotheae conspicua* Lindl. (*Podocarpaceae*) and *T. stipularis* equations for all other tree species.

The live woody biomass in the moorland was divided into two categories, independent of species. We sampled the bigger trees with identifiable main stems separately from the low lying clumps of woody vegetation. For 16 representative erect trees, we measured the basal diameter, height, and total wet-weight of the aboveground plant. For prostrate clumps of woody vegetation, we measured the surface area of six representative clumps, then harvested and weighed the aboveground biomass. Subsamples of the biomass were taken to estimate the wet-to-dry weight conversion for each category. All destructive harvesting occurred near but outside of the research watersheds.

Belowground biomass

All large roots (roots $\geq$1 cm in diameter) were harvested from 16, 1 × 1-m pits. We located pits in the forest adjacent to the research areas. Pits were dug to the bottom of the rooting zone. We washed and weighed all large roots in the field. Moisture-corrected weights were determined from subsamples of the large roots. Large root biomass of the moorland was considered negligible since we observed no large roots during the course of our extensive soil sampling in the moorland.

Small roots (roots $<$ 1 cm in diameter) were harvested along with the soil samples (see Zarin et al. 1998). We collected root samples at four random locations near the edges of the 18 vegetation plots. We excavated a 7.5 cm × 15 cm sample to the depth of 10 cm. A 5-cm diameter corer was used to remove a 10–40 cm sample and, when the soil was deep enough (5 out of 72 profiles), a 40–70 cm sample. We took the mean biomass of the four samples near each plot as the best plot-level estimate of small root biomass.

To measure small root biomass, loose soil and organic matter were washed out of the samples in the lab. Rinse water was passed through a 2 mm and a 0.5 mm sieve. Organic matter sticking to roots was removed with forceps. Root fragments on the sieves were collected. Fragments $<$ 0.2 mm in diameter and $<$ 3 mm long were lost during rinsing. To estimate the mass of lost fine roots, ten samples were first separated by hand. All the roots were dried and weighed, then the roots were washed as described above. The roots escaping the sieves accounted for less than 4% of total small root weight. Although this size class of roots represent the most rapidly cycling portion of the root biomass, it constitutes a small fraction of the total belowground biomass pool.

Statistical analysis

Two way indicator species analysis (TWINSPAN) was used to classify the plots into vegetation types. TWINSPAN is a divisive, hierarchical procedure that produces a coordinated classification of samples and species (van Tongeren 1995). The classification is based on indicator species – those species that occur mostly in one group of samples and not another. In the TWINSPAN analysis, we used the live basal area of tree species in each plot as a measure of species importance. Only divisions with eigenvalues $>$ 0.25 were maintained. In other words, we only included the most robust species associations. As a check on the classifications produced by TWINSPAN and to document fundamental gradients in species associations, we performed detrended correspondence analysis (Causton 1988) using the algorithm, DECORANA. This ordination technique arranges sites along axes on the basis of similarity in species composition (ter Braak 1995). All multivariate analyses were run in PC-ORD (McCune & Medford 1997).

Linear regression was used to develop equations that predict the dependent variable (height or mass) from a measured independent variable (typically dbh). In all cases, the variables were transformed, if necessary, to meet the assumptions of (1) a linear relationship between dependent and independent variable, (2) a normal distribution of error terms, and (3) the condition of equal error variances (Neter et al. 1990). The final regression models were those that maximized the degree of linear association between the dependent and independent variable (i.e., models that maximized adjusted R^2). For logarithmic transformations, we corrected the bias in back-transformed predictions (Sprugel 1983).

Based on the results of the species association analyses, we divided plots into vegetation types. We calculated tree density and basal area using the slope-corrected surface area (i.e., horizontal area) of the vegetation plots following the standard definition of these terms in forestry (Avery & Burkhart 1994). In contrast, we reported plot-level estimates of biomass per unit ground area to coincide with our assessment of root biomass. Statistical comparisons between types were made using parametric techniques. We calculated standard confidence intervals (95%) from simple plot-level variance for each biomass component and estimated uncertainty in total biomass as the sum of the low and high range for each component. Uncertainty in biomass estimates is discussed below.

Results

Community composition and structure

TWINSPAN classified the plots into three primary associations (Table 1): the bottomland *Fitzroya* forest, a *Pilgerodendron-Tepualia* transition zone with a significant component of *F. cupressoides* (14% of basal area), and a moorland association. The moorland consisted of a mixture of low-lying individuals of *F. cupressoides*, *P. uviferum*, and *T. stipularis* and nonarboreal species, such as *Donatia fiscicularis* J. R. et G. Forster (*Donatiaceae*) and *Astelia pumila* (G. Forster) R. Br. (*Liliaceae*). The DECORANA ordination supported the TWINSPAN classifications and identified the obvious elevational gradient in vegetation composition with *Fitzroya* forest at the bottom of the watershed and the moorland at the exposed ridgetop. Corresponding to this change in vegetation was an obvious and significant linear decrease in basal area with increasing elevation ($R^2 = 0.51$; p of slope < 0.0001). In terms of land area, bottomland *Fitzroya* forests occupied 17% of the research watersheds; transition *Pilgerodendron-Tepualia* forests occurred on 72%; and moorland ridgetops covered 11% (Figure 1).

There were significant differences in woody plant density and basal area among the three vegetation zones (Table 1). The bottomland *Fitzroya* forest had a mean basal area of 138.2 $\mathrm{m}^2\ \mathrm{ha}^{-1}$, significantly greater than the two other vegetation zones. This closed-canopy forest was dominated by *F. cupressoides* and to a lesser extent by *P. uviferum. N. nitida* and *T. stipularis* were also present at lower densities. The *Pilgerodendron-Tepualia* transition zone had half the basal area and a more open canopy but 65% more stems than the *Fitzroya* forest. Although *P. uviferum* and *T. stipularis* contributed equally to the basal area, on average *P. uviferum* trees were much larger than the much more numerous *T. stipularis*. In the moorland plots, tree basal area was 7.3 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ and mean tree height was 1.2 m (s.d. = 0.99). The average height of *T. stipularis* shrubs was 1.4 m tall (s.d. = 1.1) and clumps of woody vegetation covered 16% of the ground area.

Tree size and age structure

The trees were short relative to the diameter of their stems. Regardless of girth, tree heights reached an asymptote at 15.4 m. Absolute tree height decreased with elevation. Canopy trees in the *Fitzroya* forest were more than 60% taller than canopy trees in the *Pilgerodendron-Tepualia* forest (Figure 2). The mean height of canopy trees in the *Fitzroya* forest was 10.2 m compared to a mean height of 6.2 m in the *Pilgerodendron-Tepualia* forest (t-test, $p < 0.0001$). The tallest tree measured was a *F. cupressoides* that was 15.3 m tall. Considering the big difference in tree height, it was surprising that there was no difference in live crown ratio (height of the base of the live crown/total tree height) between forest zones. Live crown ratio was 0.68 in the *Fitzroya* forest and 0.63 in the *Pilgerodendron-Tepualia* forest (t-test, $p = 0.10$).

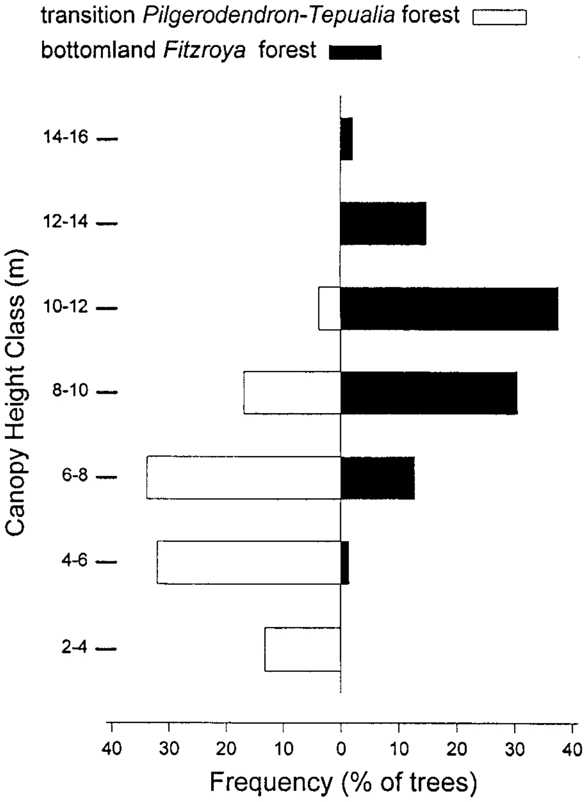

Figure 2. Height distribution of canopy-sized trees in the forested vegetation types in the research watersheds in the Cordillera de Piuchué.

Diameter distributions of the five important tree species in the forests varied markedly among species and between forest zones (Figure 3). The diameters of *F. cupressoides* in the *Fitzroya* forest had a flattened bell-shaped distribution will a long tail toward the larger size classes. *P. uviferum* trees in the *Fitzroya* forest had a more sharply peaked unimodal distribution centered in the smaller size classes with just a few trees with dbh's > 25 cm (Figures 3A and 3B). In contrast, *F. cupressoides* of any size were scarce in the *Pilgerodendron-Tepualia* forest and *P. uviferum* in this forest had a reverse J-shaped dbh distribution (Figures 3A and 3B). In both vegetation zones, *Nothofagus nitida, T. stipularis*, and *Podocarpus nubigena* had dbh distributions where there were many more small trees than large trees (Figures 3C, 3D and 3E).

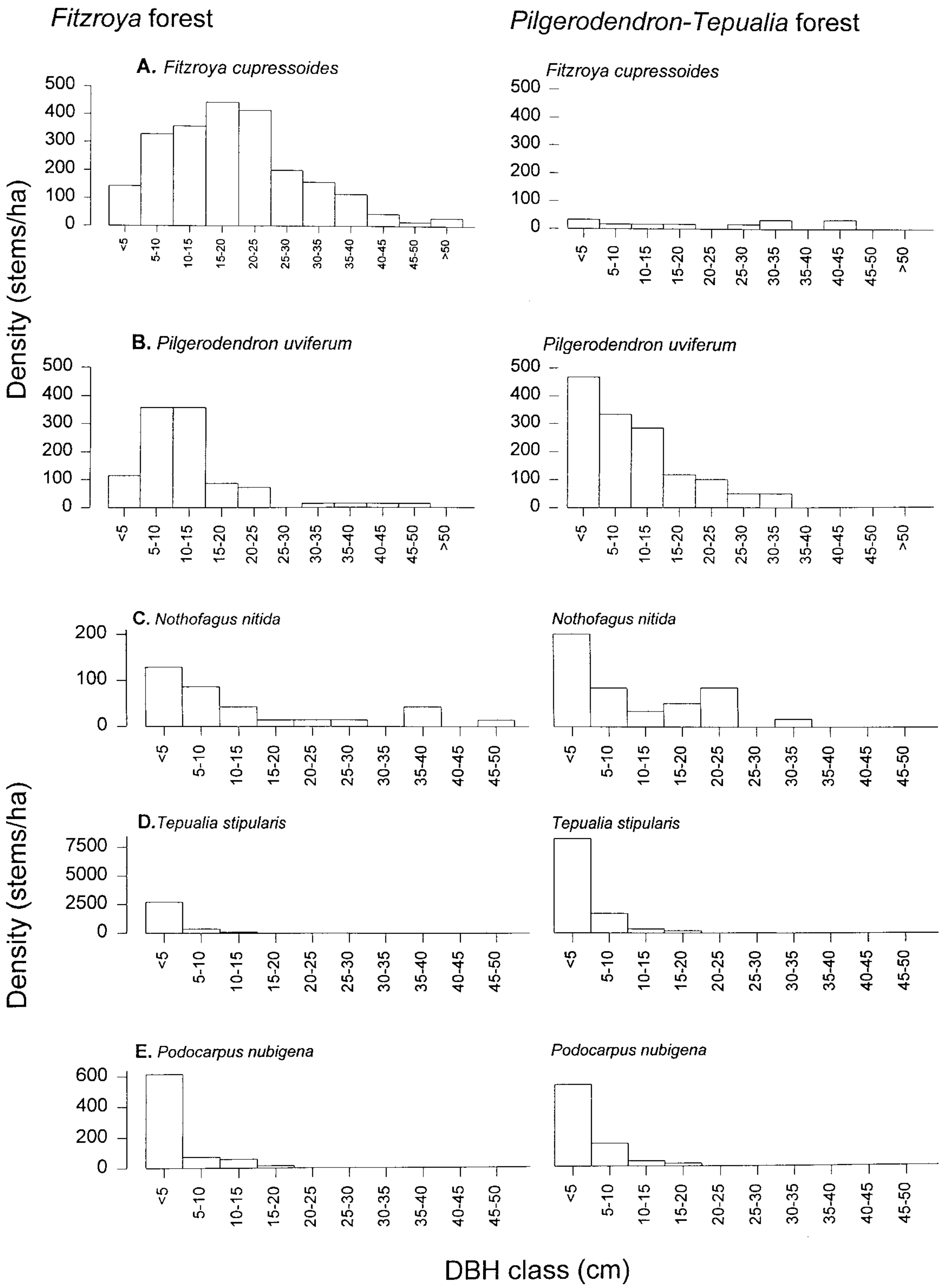

Figure 3. Comparison of the dbh (diameter at breast height) distributions of the most abundant woody species in the two forest types found in the Cordillera de Piuchué ecosystem study. (A) Dbh distributions of *F. cupressoides*. (B) Dbh distributions of *P. uviferum*. (C) Dbh distributions of *N. nitida*. (D) Dbh distribution of *T. stipularis*. (E) Dbh distributions of *P. nubigena*.

Table 1. Woody plant composition in the different vegetation types found in the research watersheds at Cordillera de Piuchué, southern Chile. Density and basal area calculated only for live trees. Basal areas for the moorland was calculated from diameters measured at the base of the trees. Means with different small case subscripts are significantly different (Tukey's HSD with family $p < 0.05$). SE is the standard error of the mean.

Forest type	Density (stems ha^{-1})		Basal Area (m^2 ha^{-1})		Dominant woody species
	Mean	SE	Mean	SE	(% basal area)
Fitzroya	9 680^{ab}	1161	138.2^{a}	20.4	*Fitzroya (67); Pilgerodendron (14)*
Pilgerodendron-Tepualia	16 029^{a}	4516	69.5^{b}	10.5	*Pilgerodendron (36); Tepualia (36)*;
Moorland	4 368^{b}	1674	7.3^{c}	2.4	*Fitzroya (45); Pilgerodendron (43)*

F. cupressoides trees in the *Fitzroya* forest in CP-2 were significantly older than comparable trees growing uphill in the *Pilgerodendron-Tepualia* zone (Figure 4, t-test, $p < 0.0001$). Ages at dbh for canopy-size *F. cupressoides* in the *Fitzroya* forest ranged from 236 to 556 yo with a mean age of 377 years (s.d. = 64 yr; $n = 40$). The oldest *F. cupressoides* in the *Pilgerodendron-Tepualia* forest was 389 yo and average age was 269 yo (s.d. = 67; $n = 20$).

Live woody biomass

Our best estimate of total live woody biomass for the research watersheds was 377 Mg ha^{-1}. Aboveground biomass accounted for 81% of the total; large roots for 7%, and small roots for 12% (Table 2). CP-2 had a higher mean biomass than CP-1 – 466 Mg ha^{-1} versus 331 Mg ha^{-1}. Most of this difference could be attributed to the contribution of the two *Fitzroya* plots in CP-2. These plots had the two largest aboveground biomass estimates in the study area (930 Mg ha^{-1} and 734 Mg ha^{-1}, Appendix 1). The *Fitzroya* forest had more than two times more aboveground biomass than the *Pilgerodendron-Tepualia* forest and almost 40 times the biomass in the moorland (Table 2). Similar to the trend in basal area, total plot biomass linearly decreased with increasing elevation ($R^2 = 0.55$; p of slope < 0.0001). In general, the absolute differences in live root biomass among vegetation types were much less than in the aboveground fraction. Despite the large differences in the total biomass among vegetation types and between watersheds, the only significant difference (defined by non-overlap of 95%CI's) was between the moorland and the forested vegetation types. There was large plot-to-plot variation in estimates of aboveground biomass, even within vegetation types (Appendix 1, Table 2).

Species contribution to aboveground biomass in each forest type tracked relative basal area with the exception of *T. stipularis* that contributed more biomass than expected based on its basal area (Table 3, Appendix 2). Compared to the conifers, *T. stipularis* wood was more dense. Since wood accounted for more than 90% of the biomass in both forests (Table 2), small changes in wood density can have a large effect on total biomass.

There were large differences in the partitioning of biomass between forest types. The *Fitzroya* forest had twice the aboveground biomass of the *Pilgerodendron-Tepualia* but less than 10% more root biomass (Table 2). In other words, the shoot to root ratio in the *Fitzroya* forest was 7.2 compared to a shoot:root ratio of 3.7 in the *Pilgerodendron-Tepualia* forest. Furthermore in the *Fitzroya* forest, the biomass of leaves and twigs was 36.6 Mg ha^{-1}. The comparable belowground component was the small roots (fine roots and their immediate support tissue) with a biomass of 40 Mg ha^{-1}. The resulting ratio of light acquiring biomass to nutrient/water acquiring biomass was 0.92. This partition ratio for the *Pilgerodendron-Tepualia* forest was 0.36 (Tables 2 and 3).

Discussion

Comparison with regional vegetation

The latitude of the Cordillera de Piuchué watersheds (42°30′ S) places them at the border of the Valdivian rainforest (37°45′ to 43°20′ S) and North Patagonian rainforest (43°20′ to 47°30′ S) districts (Walter 1973; Veblen et al. 1995). Floristic elements characteristic of both zones are present. The forested parts of the research watersheds more closely resemble the North Patagonian forest type because of the predominance of conifers such as *Fitzroya* and *Pilgerodendron* (Appendix 2). *P. uviferum* is an abundant tree in the

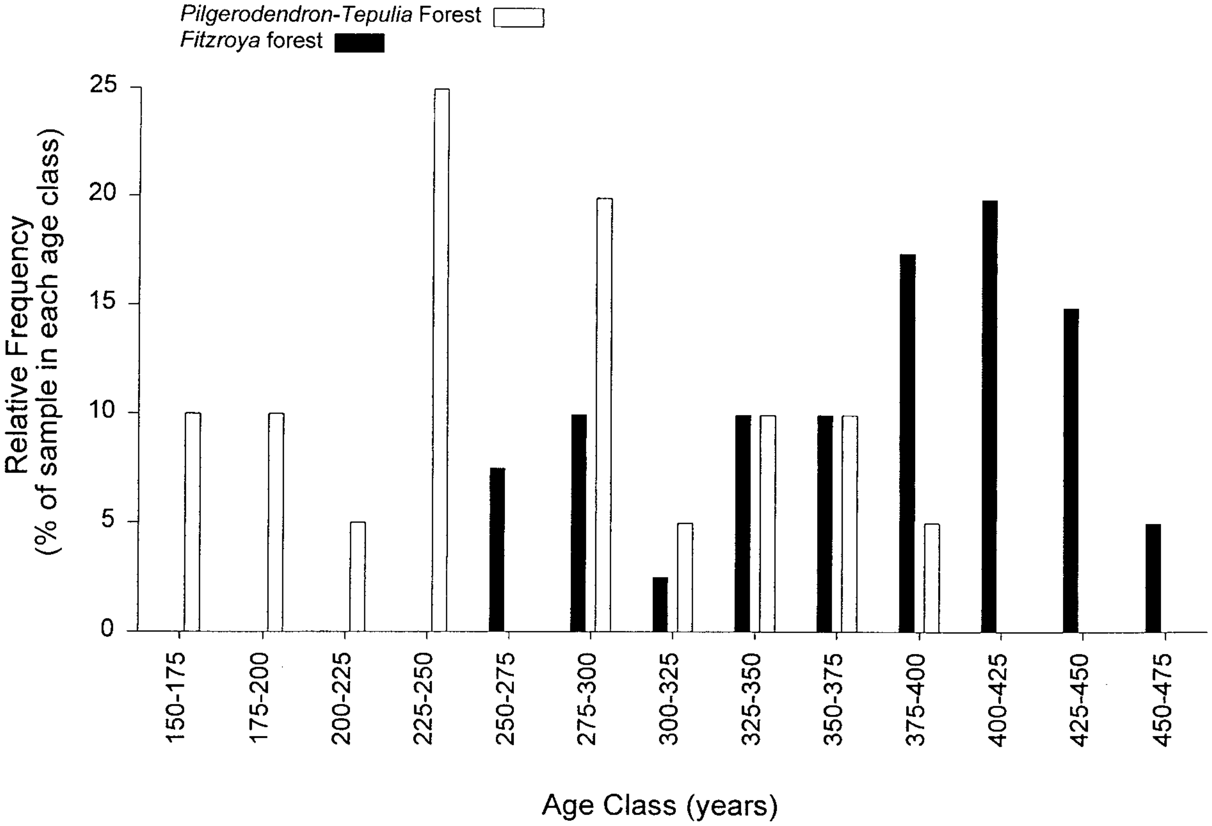

Figure 4. Comparison of the age distribution of canopy-sized *F. cupressoides* in the two forest associations in the CP-2 research watershed in the Cordillera de Piuchué.

Table 2. Summary of live biomass in the Cordillera de Piuchué Study watersheds. The 95% confidence interval for each biomass component was calculated from the simple plot-level variances. Confidence intervals for total live biomass are the sums of the low and high range estimates for each component. For each forest type, n is the number of vegetation plots. Watershed-level estimates of biomass are weighted means where weights were based on proportional surface area covered by each vegetation zone in the watershed. Large roots were defined as roots ≥1 cm in diameter; small roots were < 1 cm in diameter.

		Aboveground tree (Mg ha^{-1})		Large roots (Mg ha^{-1})		Small roots (Mg ha^{-1})		Total live biomass (Mg ha^{-1})	
	n	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
Vegetation zone									
Fitzroya Forest	7	576	387–765	40	17–63	40	33–47	656	437–875
Pilgerodendron-Tepualia Forest	6	275	123–428	25	5–44	50	31–69	350	159–541
Moorland	5	15	8–22	0	–	25	16–33	40	24–55
Watershed									
Both	18	306		25[a]		46		377	
CP-1	12	261		24[a]		46		331	
CP-2	6	396		26[a]		44		466	

[a] Large roots were sampled outside of the research watersheds. The reported means are weighted based on the contribution of each vegetation type to total watershed surface area.

Table 3. Contribution by species and part to aboveground live biomass for trees in forests of the Cordillera de Piuchué watersheds. Foliage was defined as apical shoots retaining foliage; twigs were shoots arising from branches < 1 cm in diameter; branches were shoots ≥ 1 cm in diameter; the bole was the main trunk of the tree, less the top (Vann et al. 1998).

	D. winteri	*F. cupressoides*	*Nothofagus*	*P. nubigenus*	*P. uviferum*	*T. stipularis*	Total[a]
Percent of total (%)							
Fitzroya forest	0.3	67.5	15.0	1.0	10.6	5.7	–
Pilgerodendron-Tepualia[b]	0	15.6	13.5	2.1	24.1	44.7	–
Foliage + twigs (Mg ha^{-1})							
Fitzroya forest	0.2	24.3	4.2	1.3	4.7	–	36.6
Pilgerodendron-Tepualia[b]	0	2.9	2.0	1.5	6.1	–	18.1
Branches (Mg ha^{-1})							
Fitzroya forest	0.2	13.9	9.4	1.1	2.8	–	29.0
Pilgerodendron-Tepualia[b]	0	1.9	4.8	1.3	3.4	–	16.5
Bole + root crown (Mg ha^{-1})							
Fitzroya forest	1.2	348.6	65.0	3.5	54.7	–	500.0
Pilgerodendron-Tepualia[b]	0	44.6	32.4	4.0	68.9	–	217.0

[a] *T. stipularis* was not sampled by component. Therefore the total biomass of each component includes an estimate of the contribution of *T. stipularis* based on the proportion of *T. stipularis* in the total biomass (5.7% in the *Fitzroya* forest and 44.7% in the *Pilgerodendron-Tepualia* forest).

[b] The component biomass estimates for the *Pilgerodendron-Tepualia* forest did not include one plot sampled as a moorland plot but later reclassified as a *Pilgerodendron-Tepualia* plot.

North Patagonian rainforest particularly to the south of Chiloé, and the *Pilgerodendron-Tepualia* transition forest was similar in composition and structure to coastal rainforests occurring at higher latitudes. In terms of the flora and physiognomy, the moorland at the summits was analogous to the Magellanic moorland community that occurs along the Pacific Coast of Chile south of 43° S latitude (Veblen et al. 1983, 1995; Villagrán 1988; Ruthsatz & Villagrán 1991). The vegetation gradient characterized by *Fitzroya* forest on the slopes and moorland on the more exposed and more poorly drained sites is a common feature of the landscape in the summits of the Cordillera de Piuchué. This high altitude mosaic probably resembles the older glacial landscape once found at lower elevations in Chiloé (Villagrán 1990, 1991).

Armesto et al. (1995) noted that Chilean coastal forests had a markedly different glacial history and disturbance regime than the Andean forests and therefore should be considered separate from the interior vegetation. They classified similar coastal conifer forests on Chiloé as old-growth *Fitzroya-Pilgerodendron* forests. Donoso et al. (1993) identified a coastal highland forest type in southern Chile composed of stunted *F. cupressoides* growing in nearly pure stands – an apt description of the bottomland *Fitzroya* forest in the research watersheds. Our classification was consistent with these more general descriptions of the Cordillera de Piuchué vegetation.

Biomass distribution

Our estimate of 306 Mg ha^{-1} of aboveground biomass in the Cordillera de Piuchué watersheds fell near the average aboveground biomass for temperate conifer sites in the International Biological Program (mean = 307 Mg ha^{-1}, s.d. = 272 Mg ha^{-1}, Cole & Rapp 1981). A disproportionate contributor to this watershed average was the *Fitzroya* forest – a forest that in terms of aboveground biomass (576 Mg ha^{-1}) ranked among the more massive forests in the world. High biomass forests are typically found in warm-temperate climates like Chiloé's where there is no prolonged summer drought and an absence of freezing temperatures (Walter 1973, Waring & Franklin 1979; Alaback 1991). However the *Fitzroya* forest was less massive than other temperate rainforests. For example, aboveground biomass estimates for mature *Picea-Tsuga* forests in the Coast Range of Oregon range from 761 Mg ha^{-1} (Harcombe et al. 1990) to 1286 Mg ha^{-1} (Gholz 1982). The aboveground biomass of coastal Sequoia stands in northern California can exceed 3000 Mg ha^{-1} (Westman & Whittaker 1975; Fujimori 1977). The distinguishing features of the *Fitzroya* forest were the absence of truly large trees (both in terms of height and girth) and the abundance of mid-sized trees. The majority of basal area (61%) was due to the 1749 trees ha^{-1} with dbh's between 15 and 40 cm. By comparison, the *Picea-Tsuga* stands measured by Harcombe et al. (1990) had higher tree biomass despite much lower basal areas (90–120 m^2 ha^{-1}) and much lower tree densities (230–540 trees ha^{-1}).

One likely reason for the short stature of the *Fitzroya* forest is the influence of coastal winds. Greene et al. (1992) compared tree height, annual mortality, and biomass for *Picea-Tsuga* forests along a wind disturbance gradient in northern Oregon. In the more exposed forests near the coast, trees tended to be shorter for a given diameter compared to more sheltered trees inland; annual mortality rates were more than double the rates for inland tree populations (2.8% per year vs 1.01% per year); and bolewood biomass was only 60% of inland forests (460 Mg ha^{-1} vs. 761 Mg ha^{-1}). *F. cupressoides* on the mainland is a giant conifer similar in growth-form but not absolute size to *Sequoiadendron giganteum*, Lindley (Buchholz) (*Cupressaceae*). Large *F. cupressoides* in the interior forests of South America can reach heights of more than 50 m and girths greater than 4 m (Veblen et al. 1976). Most inland *Fitzroya* forests have been disturbed by logging but judging from stumps, logs, and remaining stands, they are reportedly more massive and taller than coastal forests (Veblen et al. 1995). Certainly the trees in our study plots were considerably smaller than those on the mainland. The shallow, poorly drained soils in the watershed may also limit height growth in *F. cupressoides*.

As noted above, a steep vegetational gradient was observed at the study site that generally tracked elevation and coincident changes in exposure and soil drainage. Not only did patterns of species abundance change but also stand basal area, canopy height, and biomass decreased with elevation (Tables 1 and 2, Figure 2). While such transitions are typical for timberline environments, the abruptness of the shift in Cordillera de Piuchué was remarkable. Across a horizontal distance of < 300 m and a vertical shift of 60 m, a high biomass forest gave way to a herbaceous moorland community. The pygmy forest region of California is perhaps the most dramatic example of a terrestrial vegetation discontinuity: a place where the tallest and shortest forests in the world exist less than 30 m apart. In the pygmy forest region, the differences in vegetation are caused predominantly by soil factors such as acidity, aluminum concentration and fertility (Westman 1975). In contrast, Zarin et al. (1998) found no significant differences between the *Fitzroya* and *Pilgerodendron-Tepualia* forests in soil bulk density, pH, soil organic carbon, total N, and exchangeable cations (including Al). The differences we observed were probably an extreme instance of vegetation change along the complex elevation gradient (sensu Whittaker 1975) where gradients in both wind exposure, fire disturbance, and soil drainage presumably play important roles. Moorlands may represent ancient glacial vegetation that colonized previously exposed, barren areas (Villagrán 1990) that are now being gradually replaced by krummholz forms of the longer-lived conifer species in the more sheltered sites.

Regardless of the cause, the vegetation gradient in the research watersheds contributed to the uncertainty of our estimates of total biomass. The major sources of uncertainty were (1) errors in the allometric equations, (2) variation in biomass within a vegetation type, and (3) variation in biomass between types. Vann et al. (1998) explored the accuracy of the allometric equations given the restrictions on sampling live trees. In general, their percent standard errors of the estimates for tree biomass were no larger than those reported for similar species in similar forests (e.g., Grier & Logan 1977). They concluded that estimates of tree biomass were within 10% of the true mean for watershed-scale studies (Vann et al. 1998). The within-type variance in the aboveground biomass in the *Fitzroya* forests (coefficient of variation = 36%) and *Pilgerodendron-Tepualia* forest (cov = 53%) were comparable to those reported for a mountain beech forests in New Zealand (cov = 33%, Harcombe et al. 1998) and a coastal *Picea-Tsuga* forests in Oregon (cov = 51%, Green et al. 1990). Both of these sources of uncertainty were dwarfed by the variability in biomass among vegetation types (Appendix 1). The range of biomass estimates observed in one watershed (CP-2, 930 Mg ha^{-1} to 11 Mg ha^{-1}) was comparable to the range observed across a 350 km latitudinal transect in the Pacific Northwest that crossed eight major vegetation zones (Gholz 1982). We accounted for this variation by measuring the mean biomass for each type and then calculating a watershed average based on the proportional contribution (by area) of each vegetation type. This approach also removed any bias introduced by the fact we oversampled the *Fitzroya* and moorland vegetation types relative to their coverage in the watersheds (Figure 1).

Epiphytes, shrubs other than the ubiquitous *T. stipularis*, and herbaceous plants were excluded from our biomass calculations. Epiphytes are a conspicuous feature of the vegetation in these rainforests. Armesto et al. (1995) reported a epiphyte biomass of 4 Mg ha^{-1} and a more recent study measured an average epiphyte biomass of 8.2 Mg ha^{-1} (range 2–12 Mg ha^{-1}) in an old-growth *Fitzroya-Pilgerodendron* forest on Chiloé (Armesto et al. unpublished data). This amount represents less than 3% of live aboveground biomass in the watersheds (Table 2). Shrubs, vines, and herbs likely constitute a small proportion of the total biomass in the watersheds but could account for a relatively large fraction in the moorland plots.

A much greater proportion of live biomass was allocated to belowground tissue in the *Pilgerodendron-Tepualia* transition zone compared to the *Fitzroya* forest (Tables 2 and 3). Such an allocation pattern in biomass suggests differences in nutrient availability but Zarin et al. (1998) found no differences in soil nutrient capital between the two forest types. Both *P. uviferum* and *T. stipularis* occur in poorly drained, waterlogged soils in southern Chile (Veblen et al. 1995; Armesto et al. 1995). Differences in soil moisture could be an important environmental gradient in the watersheds. Periodic soil saturation may reduce nutrient uptake (Kozlowski & Pallardy 1997). The trees may respond to the nutrient stress by allocating more biomass to roots (sensu Tillman 1988). Alternatively, these allocation patterns may be due to inherent differences in species life histories, or aboveground biomass in the *Pilgerodendron-Tepualia* zone may be constrained by limits in stem height due to wind stress.

Forest dynamics

The unimodal dbh distributions of both conifers in the *Fitzroya* forest (Figure 3A and 3B) are typically observed for populations of shade-intolerant trees that develop following a severe, stand devastating disturbance (Oliver & Larson 1996). Both *F. cupressoides* and *P. uviferum* are considered shade-intolerant conifers (Enright & Ogden 1995; Armesto et al. 1995). The age distribution of *F. cupressoides* in the *Fitzroya* forest (Figure 4) suggests that a major disturbance occurred more than 400 years ago, followed by an extended period of recruitment. Fire is thought to be the most likely cause of coarse-scale disturbance in these coastal forests (Armesto et al. 1995; Fraver et al. 1999). The reverse J-shaped dbh distributions of *N. nitida, Podocarpus nubigena* and *T. stipularis* (Figure 3C–E) indicate that these the more shade-tolerant tree species are poised to replace the intolerant conifers in the *Fitzroya* forest in the absence of fire. However, the average longevity of *F. cupressoides* in the region (1200 years, Enright & Ogden 1995) ensures that the replacement will be a slow process.

In the *Pilgerodendron-Tepualia* transition zone, all of the major species, except *F. cupressoides*, seemed to be able to regenerate in the understory (Figure 3). Adult *F. cupressoides* were significantly younger in the transition zone than trees of the same status in the *Fitzroya* forest (Figure 4). This age difference may reflect either a delay in initial recruitment or a higher mortality rate for trees in the transition zone. The transition zone forest had a more open canopy and more standing dead trees than the *Fitzroya* forest. In relative terms, 28% of total stem basal area in the *Pilgerodendron-Tepualia* type consisted of dead stems compared to 14% in the *Fitzroya* forest. Presumably these dead trees create gaps sufficient for *P. uviferum* regeneration but not for *F. cupressoides*. Successful regeneration of *F. cupressoides* in the Andes depends on both high light and mineral soil seedbed (Lara 1991; Donoso et al. 1993). Dead tree gaps increase light availability but do not greatly disturb the soil. Perhaps it is the lack of appropriate seedbed that limits *F. cupressoides* germination in the transition forest.

Summary

The Cordillera de Piuchué watersheds had many of the ecological characteristics typical of old-growth, temperate forests. The specific group that Hedin et al. (1995) used for comparison included four sites from the eastern United States with cold temperate climates and five from the Pacific Northwest with warm temperate climates (*sensu* Walter 1973). Like the Cordillera de Piuchué, these sites were relatively stable in regard to vegetation development and floristics. With one exception, evergreen conifers were the dominant vegetation. The Cordillera de Piuchué watersheds had more live tree biomass than the cold temperate sites (typical values: 150–272 Mg ha^{-1} from Johnson & Lindberg 1992) but less than the warm temperate sites (typical values: 713–853 Mg ha^{-1}, Johnson & Lindberg 1992; Cole and Rapp 1981). In terms of community dynamics, the interaction of rare catastrophic fires and common fine-scale disturbances seemed to shape the vegetation mosaic in the Cordillera de Piuchué just as it does in the conifer forests of the Pacific Northwest (Spies & Franklin 1989). What remains to be determined is whether the atypical structure of the forests (namely, a high density of short trees) and the steep vegetation gradient materially affect biogeochemical cycling in these watersheds.

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Appendix 1. Plot-by-plot summary of live tree density, basal area, and above-ground biomass for two montane watersheds in the Cordillera de Piuchué, southern Chile. P–T refers to the *Pilgerodendron-Tepualia* dominated forest.

Plot	Vegetation type	Watershed	Density (stems ha^{-1})	Basal area (m^{2}ha^{-1})	Biomass (Mg ha^{-1})
A0	Fitzroya	CP-1	10201	91.2	350
A1	Fitzroya	CP-1	8613	119.3	510
B1	Fitzroya	CP-1	9153	149.0	585
B2	Fitzroya	CP-1	14252	132.5	560
C2	Fitzroya	CP-1	7492	73.2	364
X0	Fitzroya	CP-2	12795	237.2	930
X1	Fitzroya	CP-2	5256	164.6	734
C3	P-T	CP-1	8761	57.8	213
C4	P-T	CP-1	10443	49.2	200
D2	P-T	CP-1	18592	90.3	361
W2	P-T	CP-2	37451	87.2	347
X2	P-T	CP-2	9983	97.7	471
W3	P-T	CP-2	10942	35.0	61
B3	Moorland	CP-1	9610	12.0	24
C1	Moorland	CP-1	1112	1.1	12
D3	Moorland	CP-1	3195	9.5	13
D4	Moorland	CP-1	6813	11.8	15
V2	Moorland	CP-2	1109	2.0	11

Appendix 2. Species-by-species summary of live tree basal area, density, and frequency for two forest types in the Cordillera de Piuchué, southern Chile. For each forest type, n refers to the number of 100 m^2 plots in two research watersheds.

	Fitzroya (n=7)			*Pilgerodendron-Tepualia* (n=6)		
	Basal area (m^2 ha^{-1})	Density (# ha^{-1})	Freq. (%)	Basal area (m^2 ha^{-1})	Density (# ha^{-1})	Freq. (%)
Caldcluvia paniculata	0.2	32	14	–	–	–
Desfontainea spinosa	1.9	579	57	0.4	225	67
Drimys winteri	0.8	459	29	–	–	–
Embothrium coccineum	0.7	46	29	$<$ 0.1	35	33
Fitzroya cupressoides	93.0	2382	100	9.8	204	83
Myceugenia chrisocarpa	<0.1	16	14	–	–	–
Nothofagus betuloides	4.5	157	29	–	–	–
Nothofagus nitida	10.8	383	71	7.8	532	100
Pernettya mucronata	0.2	290	29	0.1	69	50
Podocarpus nubigenus	1.7	820	86	1.8	752	50
Pilgerodendron uviferum	19.4	1081	100	24.8	2710	100
Saxegothaea conspicua	0.1	53	14	–	–	–
Tepualia stipularis	4.8	3387	100	25.0	11502	100