*Selbyana* 22(1): 76–88. 2001.

# CROWN STRUCTURE AND BIODIVERSITY IN *FITZROYA CUPRESSOIDES*, THE GIANT CONIFERS OF ALERCE ANDINO NATIONAL PARK, CHILE

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ABSTRACT. *Fitzroya cupressoides,* or alerce, a massive conifer that occurs in southern Chile and southwestern Argentina, is known for exceptional longevity—a 3622-year crossdated chronology established the alerce as the second longest-living tree after California's *Pinus longaeva.* Despite the critical ecological significance and endangered status of the alerce, remarkably little is known about the crown habitat in these trees, including their plant and insect communities. In a preliminary assessment of alerce crown structure and plant and arthropod diversity, seven alerce individuals were climbed and surveyed in January 1998. The trunk and crown structure of each tree were measured and lianas, epiphytes, and arthropods were sampled in a series of height-stratified plots. Filmy ferns were the dominant vascular epiphytes while bryophytes, lichens, and three species of lianas were also abundant in well-developed communities. Several trees and shrubs were also discovered growing epiphytically in the alerce crowns. Arthropod diversity and abundance were very low, even compared with conifers from climatically similar habitats in the United States Pacific Northwest. Herbivory was negligible—less than 1% in all foliage samples.

*Key words:* alerce, canopy, epiphytes, arthropods, biodiversity, *Fitzroya cupressoides,* Chile

## INTRODUCTION

Ancient living trees, sometimes reaching thousands of years in age, provide rare glimpses into historic plant distribution and succession patterns as well as past climate trends (Hill & Whang 1996, Lara & Villalba 1994, Villalba 1990). Such trees also have a tremendous effect on ecosystem species composition as well as habitat structure (Leisz 1994). *Fitzroya cupressoides* (Mol.) Johnst. (Cupressaceae), or alerce, a conifer endemic to southern Chile and southwestern Argentina, grows to tremendous size (to 5 m in diameter and more than 60 m in height) and is known for exceptional longevity. A 3622-year crossdated chronology established the alerce as the second longest-living tree after California's *Pinus longaeva* D.K. Bailey (Lara & Villalba 1993). The alerce physiognomy is sim-

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ilar to that of *Sequoiadendron giganteum* (Lind.) Buchh. (giant sequoia), and timber from alerce is as valuable as that from *Sequoia sempervirens* (D. Don) Endl., California's coast redwood (Veblen et al. 1976).

Although the clearing of Chile's temperate rain forests has only recently gained the attention of the global media, mass exploitation of alerce dates back to 1599. It continued without constraints until 1976, when the dramatic loss of alerce forest and poor regeneration caused the species to be declared a national monument. Despite the ban and a listing under the Convention on International Trade in Endangered Species (CITES), illegal logging continues (Lara et al. 1999, Lara et al. 1995, Veblen et al. 1976). The rapid disappearance of this and other endemic conifers of the southern cone of South America has prompted academics and conservationists alike to call for an increase in evolutionary and ecological studies of these unique species (Wilcox 1996, Lara et al. 1995, Premoli 1994, Cooper 1992, Gilroy 1992).

Given the ecological value, great age, and endangered status of the alerce, it is remarkable how little is known about the plant and insect communities that presumably thrive in its upper crown. Rhoades (1995) points out that research in many regions has demonstrated the value of older trees as habitats for sensitive species of plants (Gustafsson et al. 1992, Goward 1992). Observations of the lower trunks of the alerce have indicated a rich canopy flora, including lianas, bryophytes, and filmy ferns (Veblen & Ashton 1982), but descriptions of the canopy species have been restricted to ground-based observations.

The general lack of information on canopy plant diversity in Chile is particularly significant given the country's biogeographical isolation and high rate of endemism. Surrounded by the Pacific Ocean to the south and west, the high Andes to the east, and the Atacama Desert to the north, Chile has the highest rate of plant endemism among continental countries in Latin America (Lara & Fraver 1997, Armesto et al. 1995). More than two-thirds of the native plants of the temperate rain forest are endemic and many are endangered (Wilcox 1996).

The temperate rain forests of southern Chile also are known to have one of the richest lichen floras in the world, although no specific information exists on the distribution of lichen genera in the alerce (Galloway 1995). The prominent ecological role of lichens in nutrient cycling and environmental monitoring (Coxson & Nadkarni 1995, Pettersson et al. 1995, Rhoades 1995) makes describing epiphytic communities a research priority for the conservation of these forests.

Because of the general ecological significance of insects and their prominence in global biodiversity inventories (Stork et al. 1997, Stork & Gaston 1990), the insect communities of alerce crowns also warrant investigation. The detailed studies of Schowalter (1995) in the conifers of the United States Pacific Northwest enable comparisons of diversity and community composition between tree species and hemispheres.

The crown structure of the alerce—the arrangement of trunk, branches, branchlets, and foliage that provides the substrate for these plant and insect communities (Moffett 2000)—has been superficially compared to that of the *Sequoiadendron giganteum,* another giant conifer that can grow for thousands of years (Veblen et al. 1976). This architecture plays a key role in defining the diversity of microhabitats available in the canopy (Clement & Shaw 1999, Sillett 1999). Vann et al. (1998) used spikes to climb and measure several juvenile alerce individuals (13–65 cm diameter at breast height [dbh] and 7–17 m in height) to develop allometric equations for biomass estimation, but the crown structure for more mature individuals has not been described.

In sum, the alerce's endangered status, the region's rapid deforestation and high rate of plant endemism, and the age and apparent architectural complexity of the alerce crown habitat provide a significant incentive to begin documenting the canopy environment of *Fitzroya cupressoides.* The purpose of this research was to a) provide a preliminary assessment of plant and insect biodiversity within alerce tree crowns and b) begin to characterize the structural patterns of these ancient crowns—the first step to mapping the canopy environment.

## STUDY SITE

The main concentration of alerce habitat is in the Valdivian rain forest of the Andean range between 41°30′S and 42°S, 500–1200 m in elevation. This region contains Chile's maximum forest biomass and tree species richness (Veblen et al. 1995). This research took place on the north shore of Lago Sargazo in Chile's Alerce Andino National Park (41°30′S, 72°35′W), at ca. 450 m in elevation (FIGURE 1). Located approximately 40 km southwest of the city of Puerto Montt in Region X, this park was established in 1982 to provide protected habitat for *Fitzroya cupressoides.* Approximately half of the Park's 39,255-ha surface area is composed of alerce habitat. Alerce individuals are scattered throughout the study site and a pure stand of young

FIGURE 1. Location of Alerce Andino National Park in Chile.

individuals exists just outside the study area—a result of a landslide more than 870 years ago (Lara 1991). Mean annual temperature is 9.3°C with a January mean of 12.9°C and an August mean of 5.7°C. Annual precipitation is high, 200–414 cm, with less rainfall in austral summer (December–February), and snowfall common May–September. Prevailing wind direction is either northwest or southwest; northwesterlies may bring intense rainstorms (maximum ppt. 130–177 mm in 24 hours).

Because of the rugged topography (with slopes commonly in excess of 50 degrees), landslides are a significant element within the disturbance regime. Soils are classified as volcanic andisols. Slow-growing and shade intolerant, the alerce at this site depend upon a catastrophic mode of regeneration. Landslides, volcanic ash or lava deposits, or other land-clearing events allow the slow-growing alerce to establish and dominate until they are gradually displaced by fast-growing broadleaf trees—a process that can take more than 2000 years (Lara et al. 1999, Veblen et al. 1995, Lara 1991). Other tree species in this mixed broadleaf evergreen forest include *Nothofagus nitida* (Phil.) Krasser, *Saxegothaea conspicua* Lindl., *Laureliopsis philippiana* (Looser) Schodde, *Tepualia stipularis* (H. & A.) Griseb., *Crinodendron hookerianum* Gay, *Weinmannia trichosperma* Cav., *Podocarpus nubigena* Lindl., and *Amomyrtus luma* (Mol.) Legr. & Kausel. The understory is dominated by *Chusquea* sp. (bamboo).

## METHODS

In January 1998, seven *Fitzroya cupressoides* trees were selected along a 1-km stretch of rugged terrain surrounding Lago Sargazo. Four large individuals (224–260 cm dbh) and three intermediate size individuals (63–98 cm dbh) were rigged and climbed using a crossbow and single rope technique (Perry 1978). Tree core samples taken throughout the study site showed that the four large individuals (more than 2 m dbh) had an estimated minimum age of 1975 years, while the three smaller trees (less than 1 m dbh) were estimated to be 284–871 years old. These estimates represent minimum ages because cores often did not reach the center of the trunk, or the trunk's center was rotten. One of the larger trees was briefly sampled for vascular plants while the other six were sampled in the three phases which follow.

### Crown Structure

Height and dbh were measured for each tree. Height, diameter, azimuth from trunk, and branch-type labels (dead, foliated, and upward-growing) were recorded for every branch. The height at attachment and maximum height were recorded for large, upward growing (codominant) branches. Trunk diameter was recorded at 5 m intervals.

### Canopy Plant Sampling

Canopy plants (epiphytes and vines) were sampled in the upper crown, middle crown, lower crown, on the exposed trunk below the crown, and on the base of the trunk. At a specified height in each of the three crown regions, voucher specimens of epiphytes were removed from a minimum of three 0.5 $m^2$ plots. Height,

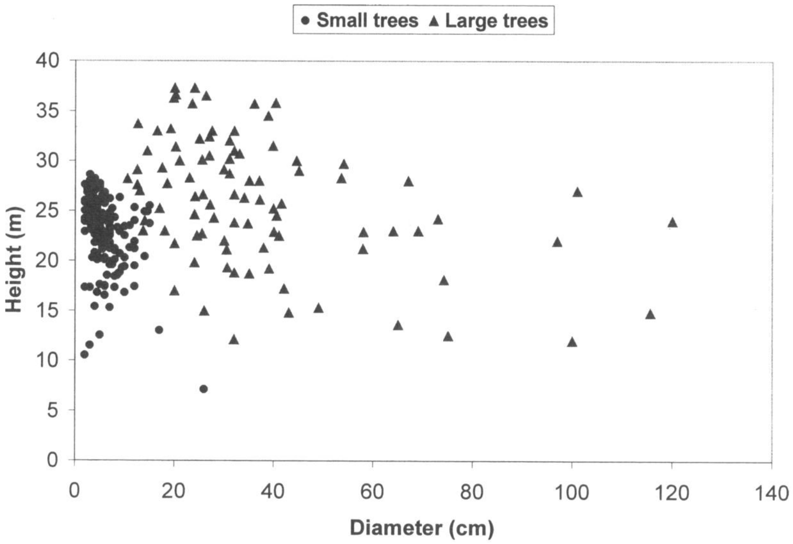

FIGURE 2. Scatterplot of branch height vs. branch diameter for large and small sample trees.

diameter, and substrate type (i.e., foliage, branch, branch crotch, dead branch, trunk) were recorded for each of these plots. Percent cover estimates were recorded for all epiphyte functional groups present in the plot, and vascular species were estimated individually. For plots on the exposed trunk below the crown, epiphytes were sampled on opposite sides of the trunk. On the base of the trunk and contiguous to the ground, 2 m$^2$ plots were established on the north, south, east, and west sides of the tree. For comparisons with ground flora, 2 m$^2$ plots also were established 5 m to the north, south, east, and west of each sample tree, and a vegetation inventory of trees, shrubs, lichens, mosses, and vines was recorded for each plot.

Filmy ferns were identified in the lab by Diego Alarçon, Ingeniero Forestal at the Universidad Austral de Chile (VALD), where the ferns collected in this study are housed. All other vascular plants were identified in the field by Alarçon. Bryophytes were identified from collected specimens by Carlos Lehnebach of the Universidad Austral de Chile, and are housed at the University of Washington Botany Department herbarium (WTU). Lichens were identified from collected specimens by Roger Rosentretter, Bureau of Land Management, Boise, Idaho, except for *Hypogymnia* specimens, which were identified by Bruce McCune, Oregon State University, Corvallis, Oregon. Lichen specimens are housed in the University of Washington Herbarium (WTU).

### Arthropod Sampling

Alerce branchlets 0.5–1.0 m in length were bagged and removed from the upper, middle, and lower branches of each tree. Each branchlet sample was surveyed intensively by magnifying lens, leaflet by leaflet, during periods of ca. 3 hours per sample. All arthropods were counted and collected, and leaf loss from herbivory was estimated to the nearest percent. Because of the remoteness of the research site, all surveying and sorting had to be completed in the field, making it impossible to identify and procure all individuals of the smallest arthropod species. Arthropods were identified from collected specimens by Mark Moffett, David Furth, and Natalia Vandenberg, and are housed at the Museum of Vertebrate Zoology, University of California, Berkeley.

## RESULTS

### Structure

Tree heights ranged from 28–42 m and dbh from 63–259 cm. The number of branches per tree was 16–71, with codominant, upward-growing branches (several more than 12 m in length) accounting for more than half of the branch structures in the larger trees. Branch diameter averaged 41 cm (maximum 120 cm) for the large trees and 6 cm (max. 26 cm) for the smaller trees (FIGURE 2). Dead branches accounted for ca. 19% of all branch structures. The average

TABLE 1. Crown structural characteristics of large and small alerce individuals, Chile, January 1998.

| Crown architectural characteristics | Large (3 trees) | Small (3 trees) |
|---|---|---|
| Height (m) | 38 | 30 |
| dbh (cm) | 245 | 76 |
| Branches (no.) | 30 | 55 |
| Codominant branches (no.) | 17 | 1 |
| Max length of codominants (m) | 15 | 1 |
| Dead branches (no.) | 7 | 7 |
| Dead branches (%) | 24 | 13 |
| Ave. branch diameter (cm) | 41 | 6 |
| Minimum branch diameter (cm) | 17 | 2 |
| Maximum branch diameter (cm) | 103 | 16 |
| Crown depth (m) | 22 | 18 |

crown depth (distance between treetop and lowest branch) was 20 m (TABLE 1).

## Canopy Plants

Of 83 species found in the study plots, 50 were in the canopy. Nine filmy fern species, five vines, two shrubs, two tree species, most of the lichen species (15 species), and most of the bryophytes (17 species) were found in the canopy. For an overall vegetation species list, see TABLE 2.

### Lianas

The canopy plant vegetation was dominated by the vascular lianas *Griselinia racemosa* (Phil.) Taub., *Philesia magellanica* Gmel., and *Pernettya insana* (Mol.) Gunckel. Of these, *G. racemosa* was the most ubiquitous and aggressive climber, commonly found at more than 30 m. Lianas were absent in one of the sample trees (Tree E), possibly a result of shading from an adjacent cluster of more robust alerce crowns (FIGURE 3).

### Epiphytes

The epiphyte communities were dominated by filmy ferns (*Hymenophyllum spp.*). Bryophytes and lichens also were abundant throughout the crown. Larger substrates contained samples of all of the above in well-developed communities. Two tree species, *Tepualia stipularis* and *Weinmannia trichosperma,* were found growing 34 m off the ground in the deep soil mats in the alerce crowns, as were two shrubs, *Desfontainia spinosa* Ruíz & Pav. and *Pseudopanax laetevirens* (Gay) Harms. (TABLE 2).

### Trunk base vegetation

As with all substrates sampled, the tree trunk bases contained a variety of mosses, filmy ferns, and lichens—although they contained a greater abundance of lichens than were found on the ground. We found a greater diversity of trunk base vegetation on the larger sample trees, with four more tree species, three more shrub species, and one more vine species than were found on the smaller trees.

### Ground vegetation

The percent cover of mosses and filmy ferns was consistently high in the ground plots. In addition to a variety of lichens, mosses, and filmy ferns, terrestrial vegetation around the sample trees was characterized by 12 tree species, three shrub species, six species of vine, and a ground fern—*Blechnum penna-marina* (Poiret) Kuhn. Ground vegetation around the large sample trees was similar to that around the small sample trees but featured six more tree species.

### Stratification

Little stratification of bryophytes or lichens was evident within the alerce tree crowns, although lichens were scarce in the trunk base and ground plots. The most abundant species of filmy ferns grew throughout the tree crowns, while three species were confined to the trunk base. Percent cover of bryophytes (lumped with the filmy ferns) on branches and trunks showed no significant correlation with height. Of the 18 bryophyte species present, one (*Orthodontium australe* Hook.f. & Wils.) was confined to the trunk base, four were found from the trunk base to the tree top, and seven others were confined to the canopy region but had 16–26 m height ranges (average crown depth for these trees was only 20 m). One species, *Porella chilensis* (L.S.L) Trev., however, was found in three trees of dramatically different structure and light regimes; yet in each case it was restricted to a height of 21–24 m.

### Large vs. small trees

Canopy plant communities differed with tree size (i.e., age). Among the most commonly found bryophyte species in alerce, *Bazzamia peruviana* (Ness) Trevis, *Neolepidozia seriatitexta* (Steph.) Fulr., and *Dicranoloma* sp. were found twice as often in the larger, older sample trees. Conversely, *Lepicolea* spp. and *Macrocoma sullivantii* (C. Muell.) Grout. were found almost three times as often in the smaller sample trees. The most abundant lichen species (*Bunodophoron* sp., *Leifidium* sp., and *Usnea* sp.) were found predominantly in the large trees, while *Hypogymnia subphysodes* was found exclusively in the large trees. The small sample trees had a generally depauperate lichen flora but boasted several *Pseudocyphellaria* species not present in the large trees. Among the filmy ferns, the most abundant species, *Hymenophyllum cuneatum*

Kunze, was found equally in large and small trees. *Hymenophyllum darwinii* Hook.f.ex Bosch and *H. dentatum* Cav., however, were found exclusively in the large trees, while *H. pectinatum* Cav. was found exclusively in the small trees. The two shrubs (*Desfontainia spinosa* and *Pseudopanax laetevirens*) and two tree species grew in the upper crowns of the large trees only.

### Canopy Arthropods

Alerce foliage harbored an extremely depauperate arthropod fauna, with 178 individuals per kg of dry branch mass. Half of these were scales and mites. Mites were difficult to collect under field conditions, and thus unfortunately could not be distinguished by taxon or feeding mode. Based on visual inspection, however, species diversity for mites was high.

The small numbers made trends difficult to discern. Little evidence was found of community stratification except for perhaps a slightly higher abundance of spiders on the lower branches (height data for scale insects were ignored because most individuals sampled occurred in a few very localized clumps). Tree size (i.e., age) did seem to make a difference for certain insect taxa. Cercopids (froghoppers) and staphylinids (rove beetles) were more abundant in the smaller trees, while psocids (booklice) and aphids were relatively numerous on the large trees (TABLE 3). The collembola and coleoptera included representatives of a variety of families—a marked abundance of staphylinids occurred in coleoptera but otherwise none were dominant.

Spiders were numerous in the samples, with free-roaming taxa accounting for 73% of specimens mature enough to be identified. Curiously only one salticid (jumping spider) specimen was found in the bagged branches. The web-dwellers included araneids, theridiids, and hahniids.

Ants were present in the alerce crowns but never in the branch samples themselves. Instead, a single species of *Lasiophanes* occurred in the soil mats and under the bark on thicker branches of large trees. Because of time constraints of the foliage methodology, soil mats and trunk fauna remain mostly unsurveyed, although large cockroaches, isopods, centipedes, and other arthropods were present. Suspended soils commonly reached at least a decimeter thick on the most massive branches and in branch crotches.

Herbivory was invariably less than 1% of leaf surface area. Occasionally, small patches of leaf scales at the branchlet tips (ca. 1 cm long) showed a detectable level of leaf area lost (surface scarring perhaps resulting in a loss of an average of 3–10% of mass per leaf), apparently from a specific, though unrecognized herbivore.

## DISCUSSION

### Structure

The large, older trees (ca. 1975–2500 years old) had a much more complex architecture than did the smaller, younger trees. Massive, codominant branches were a major feature of crown structure in the large trees, often blurring the line between trunk and branch by carrying foliage upward and outward, well away from the main trunk. As a result, the crown was often characterized by large concentrations of foliage scattered throughout a very broad matrix and separated by large, open gaps.

The upward *and* outward orientation of these alerce branches complicates the task of assigning terms to crown structures. Large, old conifers in North America such as *Sequoia sempervirens, Thuja plicata* Donn., and *Sequoiadendron giganteum* are known to develop many significant codominant branch structures. Because they often grow directly upward and mimic the main trunk in growth pattern and function, these structures have been described as trunk reiterations (Sillett 1999, Sillet et al. 2000, Sillett & Van Pelt 2000). As Hallé (1995) described, reiteration is a process in which a tree simply "duplicates" its basic architectural structure as it grows branches. The reiterations described by Sillett (1999) are examples of how Hallé's theory of reiteration may be applied to conifers, trees that normally grow as one single architectural unit (Hallé 1995).

Although many examples of trunk reiteration occurred in the alerces we studied (FIGURE 4), many of the codominant structures of these alerce specimens are not so easily categorized—they grow up and away from the trunk much like the large branches of hardwoods such as *Nothofagus* or *Quercus*. Defining a structure on the continuum between trunk-like and branch-like could have a significant effect upon microhabitat definition. The extreme variability in the alerce crowns suggests the need for an expanded terminology that suits the highly variable set of growth characteristics in both gymnosperms and angiosperms.

In contrast, the smaller, younger alerce trees (ca. 284–871 years old) carried the symmetrical, conical crown characteristic of most conifer species. Although crown depth was similar to the older, larger trees, the branch structures were smaller, more numerous, and carried the foliage in symmetrical patterns close to the trunk (TABLE 1).

TABLE 2. Overall vegetation species list (asterisk indicates presence in the canopy), Chile, January 1998.

| Taxonomic or functional group | Family | Genus/Species | Common name |
|---|---|---|---|
| Epiphytic Ferns | Grammitidaceae | *Grammitis magellanica* Desv.* | Helecho palito |
| | Hymenophyllaceae | *Hymenoglossum cruentum* (Cav.) K. Presl* | Seda de la Luma |
| | | *Hymenophyllum caudiculatum* Mart. var. *productum* | Pallante chilote |
| | | *Hymenophyllum cuneatum* Kunze var. *cuneatum** | Helecho película |
| | | *Hymenophyllum darwinii* Hook.f.ex Bosch* | Helecho película |
| | | *Hymenophyllum dentatum* Cav.* | Chu-chu-lahuén |
| | | *Hymenophyllum dicranotrichum* (K. Presl) Hook. ex Sadeb. | Helecho película |
| | | *Hymenophyllum falklandicum* Baker* | Helecho película |
| | | *Hymenophyllum ferrugineum* Colla. var. *donatii* Looser | Helecho película |
| | | *Hymenophyllum ferrugineum* Colla. var. *ferrugineum* | Helecho película |
| | | *Hymenophyllum krauseanum* Phil. | Helecho película |
| | | *Hymenophyllum pectinatum* Cav.* | Helecho película |
| | | *Hymenophyllum secundum* Hook. & Grev. | Helecho película |
| | | *Hymenophyllum seselifolium* K. Presl | Helecho película |
| | | *Hymenophyllum tortuosum* Hook. & Grev. var. *glomeratum* Diem & J. Licht.* | Helecho película |
| | | *Hymenophyllum tortuosum* Hook. & Grev. var. *tortuosum* | Helecho película |
| | | *Serpyllopsis caespitosa* (Gaudich.) C. Chr. var. *caespitosa** | Helecho película |
| Ground ferns | Blechnaceae | *Blechnum penna-marina* (Poiret) Kuhn | Helecho pinque |
| | Gleicheniaceae | *Gleichenia quadripartita* (Poiret) T. Moore | Helecho palma, Yerba Ioza |
| Vines | Bignoniaceae | *Campsidium valdivianum* (Phil.) Skottsb.* | Voqui blanco |
| | Cornaceae | *Griselinia racemosa* (Phil.) Taub.* | Voqui-lilinquén |
| | Ericaceae | *Pernettya insana* (Mol.) Gunckel* | Hued-hued |
| | Gesneriaceae | *Asteranthera ovata* (Cav.) Hanst. | Estrellita |
| | | *Mitraria coccinea* Cav. | Botellita |
| | | *Sarmienta scandens* (J.D. Brnadis) Pers.* | Medallita |
| | Philesiaceae | *Luzuriaga polyphylla* (Hook.) Macbr. | Quilineja |
| | | *Philesia magellanica* J.F. Gmel.* | Coicopihue |
| Shrubs | Araliaceae | *Pseudopanax laetevirens* (Gay) Harms.* | Traumén, Sauco del diablo |
| | Desfontainiaceae | *Desfontainia spinosa* R. & P.* | Taique |
| | Elaeocarpaceae | *Crinodendron hookerianum* Gay | Chaquihue, Polizonte |
| | Ericaceae | *Gaultheria phillyreifolia* (Pers.) Sleumer | Chaura |
| | | *Pernettya pumila* (L.f.) Hook. | Chaura |
| | Poaceae | *Chusquea* sp. (*Chusquea* cf. *macrostachya* Phil.) | Quila |
| Trees | Cunoniaceae | *Caldcluvia paniculata* (Cav.) D. Don | Tiaca |
| | | *Weinmannia trichosperma* Cav.* | Tineo |
| | Cupressaceae | *Fitzroya cupressoides* (Molina) I.M. Johnston | Alerce, Lahuán |
| | Fagaceae (Nothofagaceae) | *Nothofagus dombeyi* (Mirbel) Oersted | Coihue |
| | | *Nothofagus nitida* Phil. Krasser | Coihue de Chiloé |
| | Monimiaceae | *Laureliopsis philippiana* (Looser) Schodde) | Tepa |

TABLE 2. Continued.

| Taxonomic or functional group | Family | Genus/Species | Common name |
|---|---|---|---|
| | Myrtaceae | *Amomyrtus luma* (Mol.) Legr. & Kausel | Luma |
| | | *Tepualia stipularis* (H. & A.) Griseb.* | Tepú |
| | Podocarpaceae | *Podocarpus nubigena* Lindl. | Mañío macho |
| | | *Saxegothaea conspicua* Lindl. | Mañío hembra |
| | Proteaceae | *Embothrium coccineum* J.R. & G. Forster | Notro, Ciruelillo |
| | | *Gevuina avellana* Mol. | Avellano |
| | | *Lomatia ferruginea* (Cav.) R. Br. | Romerillo, Fuinque |
| | Winteraceae | *Drimys sinteri* J.R. & G. Forster | Canelo |
| Bryophytes | Bryaceae | *Orthodontium australe* Hook.f. & Wils. | |
| | Dicraneaceae | *Chorisodontium aciphyllum* (Hook.f. & Will.)* | |
| | | *Dicranoloma australe* (Besch.) Par.* | |
| | | *Dicranoloma menziesii* (Tayl.) Par.* | |
| | | *Dicranoloma* sp. (Musci)* | |
| | Hepaticae | *Bazzamia peruviana* (Ness) Trevis* | |
| | | *Clasmatocollea cucullistipula* (Steph.) Grolle* | |
| | | *Clasmatocollea gayana* (Mont.) Grolle.* | |
| | | *Chyloscyphus valdiveinsis* Mont.* | |
| | | *Heberta* sp.* | |
| | | *Lepicolea ochroleuca* Spreng.* | |
| | | *Lepicolea rigida* (Denot.) Scott* | |
| | | *Lepidolaena menziesii* (Hook) Travis* | |
| | | *Neolepidozia seriatitexta* (Steph.) Fulr.* | |
| | | *Porella chilensis* (L.S.L) Trev.* | |
| | | *Schistochila* sp.* | |
| | | *Trichocolea elegans* Lehm.* | |
| | Orthotrichaceae | *Macrocoma sullivantii* (C. Muell.) Grout.* | |
| Lichens | | *Bunodophoron australe** | |
| | | *Bunodophoron insigne** | |
| | | *Bunodophoron* sp.* | |
| | | *Coelocaulon aculeatum** | |
| | | *Coelocaulon* sp.* | |
| | | *Hypogymnia subphysodes** | |
| | | *Imshaugia* sp.* | |
| | | *Leifidium tenerum** | |
| | | *Platismatia* sp.* | |
| | | *Protousnea* sp.* | |
| | | *Pseudocyphellaria coerulescens* | |
| | | *Pseudocyphellaria divulsa** | |
| | | *Pseudocyphellaria glabra** | |
| | | *Pseudocyphellaria imbricatula** | |
| | | *Sticta ainoae** | |
| | | *Sticta weigelii* | |
| | | *Usnea* sp. | |
| | | *Usnea subcapillaris* | |

In general, compared to North American conifers of similar stature, the alerce trees had far fewer branches, a greater percentage of codominant structures, and a lower percentage of dead branches. The crown had half the depth of old-growth *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) trees of similar height (Clement & Shaw 1999), but the alerce branches had mas-

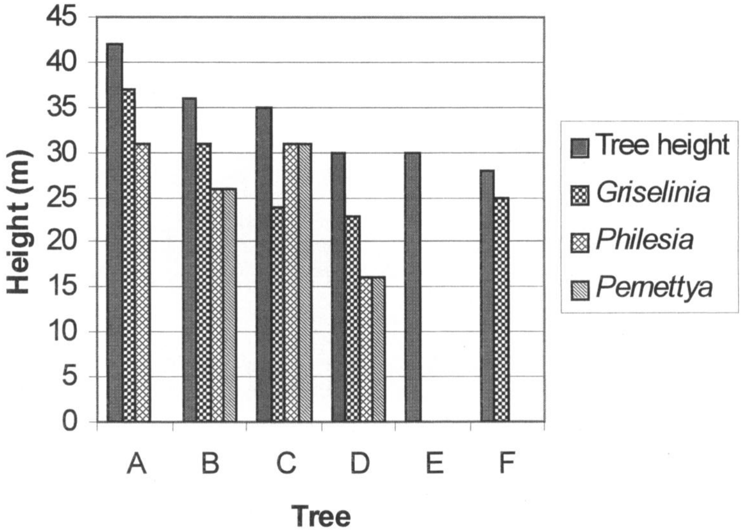

Figure 3. Maximum height attained by canopy vines.

sive girths. Unlike most conifers (e.g., Clement & Shaw 1999, Pike et al. 1977), the alerce showed no strong correlation between branch height and branch diameter. Structurally, the alerce most closely resembles the *Sequoiadendron giganteum* for massive branches and broad crown architecture and old-growth *Thuja plicata* and *Sequoia sempervirens* for the presence of numerous codominant branch structures (Figure 4) (Sillett et al. 2000, Sillett & Van Pelt 2000).

## Canopy Plants

Lianas were ubiquitous and persistent from the ground up. No vines in this site were seen connecting tree crowns or crossing open areas between large branches in the same tree. Rather, the growth habit was appressed to the bark, with leaders often hidden deep within bark fissures and in areas of wood decay. The climbing vines that dominated the canopy plants (particularly *Griselinia racemosa* and *Philesia magellanica*) also were abundant in the ground samples, which supported a greater diversity of vine species than did the canopy. In contrast, native lianas are generally absent from temperate rain forests of the Pacific Northwest region of the United States.

Four species of trees and shrubs that ordinarily are considered terrestrial thrived in the upper alerce crowns. Even a 4-m tall *Tepularia stipularis* showed no sign of stress. Other alerce crowns supported trees of much more considerable stature—in some cases creating a double-crown effect. One of the shrubs found growing as an epiphyte, *Pseudopanax laetevirens,* has the

Table 3. Crown arthropod abundance (no. individuals/kg branch mass). Canopy height data combines data from small and large trees, tree size data combines all three height samples per tree, Chile, January 1998.

| | Trees | | Crown | | |
|---|---|---|---|---|---|
| | Large | Small | Upper | Middle | Lower |
| Mites | 44.2 | 59.1 | 63.2 | 44.3 | 43.5 |
| Spiders | 21.7 | 21.3 | 17.1 | 17.7 | 29.7 |
| Psocids | 21.0 | 0.0 | 13.9 | 114 | 26.6 |
| Cercopids | 12.3 | 29.6 | 20.3 | 26.6 | 14.9 |
| Aphids | 14.5 | 2.4 | 12.8 | 7.6 | 5.7 |
| Scales | 12.3 | 57.5 | 73.8 | 22.8 | 0.0 |
| Staphylinids | 0.0 | 7.4 | 4.3 | 51 | 1.1 |
| Other beetles | 5.1 | 4.1 | 3.2 | 2.5 | 8.0 |
| Lepidoptera | 3.6 | 2.5 | 5.4 | 1.3 | 2.3 |
| Diptera | 1.4 | 1.6 | 0.0 | 2.5 | 2.3 |
| Colembola | 9.4 | 9.9 | 9.6 | 7.6 | 12.6 |

ability to send roots to the ground and grow as a hemi-epiphyte, but in these plots was not seen to do so. It is not unusual to find terrestrial plants growing as accidental epiphytes in the canopy (Benzing 1995). *Vaccinium* sp. and *Tsuga heterophylla* (Raf.) Sarg. are common in the canopy of old-growth stands of the Pacific Northwest (D. Shaw pers. obs.). Studies in the coast redwoods of California have identified at least nine species of vascular shrubs and trees growing aloft (Sillett 1999, Sillett & Van Pelt 2000).

In contrast to the robust climbing lianas found in the alerce crowns, the epiphyte assemblage was dominated by small, delicate, filmy ferns (Hymenophylaceae) with leaves only one cell thick. The filmy ferns grew in close association with bryophytes, sharing similar substrates and aspects. Abundant in wet tropical forests, the Hymenophylaceae are generally not present in the temperate forests of North America, although one species has been recorded in the wet coastal forests of southeast Alaska (S. Sillett pers. comm.). In the alerce crowns, their presence dramatically increased the biodiversity of the canopy environment.

Bryophytes and filmy ferns were abundant throughout the crown with none of the stratification evident in bryophytes of the Pacific Northwest (Clement & Shaw 1999), a likely result of the extreme humidity and high rainfall of the study site. The lichen flora and several species of both bryophytes and filmy ferns were more abundant in either the large or small sample trees. Because the lack of a vertical gradient disguises any potential successional pattern in these plants, the difference in microclimate between the open, drier crowns of the large trees and the more contained, conical crowns of the smaller trees may be the best explanation for this effect.

Unlike many conifers in temperate rain forests of North America, which have a thick cover of pendulous lichens in their outer crowns, we found little or no epiphyte growth on the terminal branches of alerce. Epiphytes were concentrated on major horizontal branches and branch crotches, some of which had deep soil pockets. This epiphyte distribution is similar to that within *Sequoia sempervirens* tree crowns (Sillet 1999).

Adjacent angiosperm trees, particularly *Nothofagus,* appeared to support a much higher epiphyte biomass then the alerce, possibly a result of differences in bark texture and chemistry but also likely a function of the more protected, shaded quality of the moist broadleaf crowns. Many *Nothofagus* also contained parasitic mistletoes, noticeably absent from the alerce crowns.

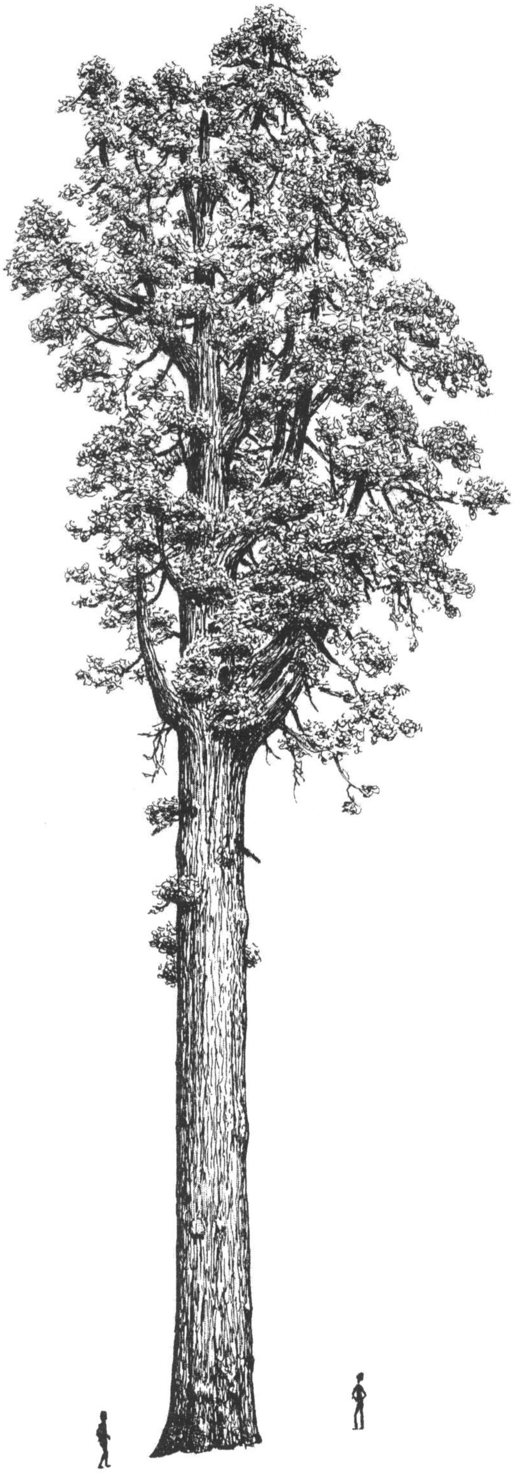

FIGURE 4. Sample tree A. Height 42 m, dbh 224 cm, minimum age 1925 years. Sketch by Dr. Robert Van Pelt.

The higher diversity of tree species found in the ground samples around the larger trees was possibly a result of increased light penetration through the characteristically fragmented crowns of the older trees. The vegetation clinging to the trunk bases was more similar to the terrestrial vegetation than the upper canopy flora, limiting the utility of using trunk base flora to predict that of the canopy. This quality reiterates a basic tenet of canopy methodologies: sample where the epiphytes under study are rather than using proxy substrates (McCune 1990).

## Canopy Arthropods

Canopy arthropod composition is likely to be highly seasonal at the latitude of this alerce stand and can be expected to change from one year to the next (for examples of seasonality and yearly unpredictability for northern hemisphere conifers, see Schowalter (1995) and Ozanne (1996). Our data can only roughly suggest the mid-summer arthropod community at this site.

Densities of branch-dwelling arthropods on alerce were extremely low, averaging 178 individuals per kg of dry branch weight. This compares, for example, to twice that figure for old-growth and mature Douglas-fir crowns in Oregon (Schowalter 1995) and for western red cedar in Washington at its lowest seasonal level (Schowalter & Ganio 1998). False spider mites common on western red cedar and incense cedar, however, are hidden in the leaf scales (T. Schowalter pers. comm.). If our field-based methods undersampled hidden species, overall arthropod densities on alerce may have approached those found on these North American conifers. No specimens in bagged samples exceeded 4 mm in length (some larger species were collected individually in the trees).

The diversity of arthropod species was likewise exceptionally low. While the alerce harbored an abundance of arachnid species (especially mites, which unfortunately could not be enumerated), most insect orders were represented by only two or three morpho-species, with about 50 insect species in all samples combined.

As in old-growth coniferous forests of the Pacific Northwest (Schowalter 1995, Winchester 1997), both the small and large alerces apparently support the same arthropod community, with differences in abundance for some taxa. While both alerce size classes harbored sap-sucking insects, aphids were better represented on the larger trees, cercopids and (possibly) scale insects on the smaller trees (scale insects being difficult to evaluate because their distributions were highly clumped). Although the younger alerce yielded somewhat more sap-sucking insects overall than the older trees, they were nowhere near as infested with such insects as the young (plantation) Douglas-fir examined by Schowalter (1995), which supported colonies of Adelgid aphids. Then again, the "small" alerces sampled in this study were almost as old as Schowalter's "old-growth" Douglas-firs.

Defoliators were scarce on alerce, averaging 2–6 individuals per kg for all heights and tree ages. Herbivory was virtually undetectable, except for a small percentage of leaf mass lost on small (1 cm long) branchlets (perhaps 10 or so patches per branch sample). North American conifers also show very little defoliation, in the order of 0–3% (Schowalter 1995, Schowalter & Ganio 1998). Schowalter and Ganio (1998) found herbivory levels of 0% at all heights on old-growth *Thuja plicata,* which, like alerce, is in the Cupressaceae. Detritivores were most common in large trees, with 32 individuals per kg dry weight compared to 10 in small trees (excluding mites, which were not classified). This pattern, noted for Douglas-fir by Schowalter (1995), presumably relates both to the proximity of a large pool of detritivores living in the soil or bark of the thick parts of the branches. Bark on the thickest branches is more likely to flake and decay on old trees than on young ones (see Schowalter & Ganio 1998).

Little stratification of the arthropod community was apparent, either by taxa or by functional group, perhaps because the open structure of the large trees creates a relatively uniform light, humidity, and temperature environment throughout their crowns. Spiders, however, appeared to be more abundant in the lower crown while scales were considerably more abundant in the upper crowns.

Old-growth coniferous forests of the Pacific Northwest lack a nesting arboreal ant fauna (*Camponotus* foragers are occasionally found on branch samples); instead, spiders represent the dominant predators (Gunnarsson 1990, Mason 1992). Spiders also were abundant and diverse on alerce crowns. One ant species was present, a *Lasiophanes* species that ranged onto the trunk and forest floor. Foragers of this species, numerous in tree crown humus, were never seen on the smaller branches, twigs, and leaves, and thus were absent from the branch samples.

## Biogeography

The southern temperate rain forests of Chile share many large-scale geographical, geological, climatic, and disturbance characteristics with the temperate rain forests of North America, but the evolutionary history and biogeography of these two biomes differ fundamentally (Lawford &

Alaback 1996, Veblen & Alaback 1996). Chile's biogeographical isolation has persisted since the tertiary period, when southern South America was connected with New Zealand and Tasmania via an ice-free Antarctica (Armesto et al. 1995, Arroyo et al. 1995). As a result of this historical connection with a variety of tropical and subtropical environments, many structural and botanical elements of the Chilean rain forest are distinctly tropical, subtropical, or austral in character. High levels of plant endemism and diversity, an abundance of evergreen broadleaf tree species, the thick bamboo understory, the dense canopy lianas, and the presence of thick mats of epiphytic filmy ferns set this temperate rain forest apart, botanically and structurally, from its counterpart in North America, which by comparison has remained relatively isolated from the rich species pools of lianas and filmy ferns offered by the tropics.

Recent fossil research has uncovered a new species of *Fitzroya* in Oligocene sediments of Tasmania, suggesting that research comparisons with other southern hemisphere conifers may have more biogeographical relevance than north-south comparisons (Hill & Whang 1996). North-south comparisons are useful in understanding how similar biome systems respond to changes and disturbances in their physical environment (Lawford & Alaback 1996, Mooney 1996). For example, it is not known whether temperate rain forest canopy plant communities in North and South America respond the same way to disturbances such as climate change or logging.

Conservation of these remarkable forests will require a thorough knowledge of structure and function throughout the ecosystem, including their canopy communities. Our assessment of canopy biota and structure in *Fitzroya cupressoides* tree crowns is a first step in gaining an understanding of the canopy biodiversity in Chile's rain forests. With this study as a preliminary road map, we encourage comparative research on structure and biodiversity in a variety of canopy environments in the forests of this region. Study opportunities include the *Nothofagus* and other broadleaf crowns, rare conifers such as *Pilgerodendron uviferum* (D. Don) Florin, and the coastal populations of *Fitzroya cupressoides.*

## ACKNOWLEDGMENTS

The authors thank the National Geographic Society's Committee for Research and Exploration for funding the field research for this study. We also thank Robert Van Pelt for his superb drawing; Yuber Reyes, a Park Ranger for Parque Nacional Alerce Andino, for his enthusiastic support and assistance in the field; David Furth and Natalia Vandenberg for identifying larvae; Carlos Lehnebach for bryophyte identifications; and Roger Rosentreter and Bruce McCune for lichen identifications. Special thanks go to Timothy Showalter and Stephen Sillett for their helpful comments on the manuscript.

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