Regeneration and stand dynamics of *Fitzroya cupressoides* (Cupressaceae) forests of southern Chile's Central Depression

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Abstract

Several populations of *Fitzroya cupressoides* (Mol.) Johnst. (Cupressaceae, common name "alerce"), a threatened, long-lived conifer endemic to southern Chile and parts of Argentina, have recently been found in Chile's Central Depression, where the species was thought to have been extirpated. The objective of this study was to determine, on eight sites in the Depression, *Fitzroya*'s regeneration behavior in relation to disturbance, its substrate and cover requirements for establishment, and whether regeneration is by seed or vegetative means. This objective required inspection of tree age-class distributions, analyses of microsite conditions and spatial distributions of *Fitzroya* individuals, and genetic analysis of *Fitzroya* trees using random amplified polymorphic DNA (RAPD) analysis. Age-class distributions indicated a "catastrophic" regeneration mode, in which seedling establishment follows stand-devastating disturbance, such as fire. Regeneration was both by seed and vegetative means (root sucker sprouting and layering), although overall, vegetative reproduction was more prevalent (63% of all regeneration). Regeneration from seed occurred primarily under open canopies (<40% cover) and on substrates of humus, moss beds, and coarse woody debris. Spatial analyses revealed clumping at various scales for *Fitzroya* seedlings, saplings, and trees. Several obvious clumps of trees were assumed to be sucker sprouts from cut stumps; however, RAPD analyses indicated they were of seed origin. Such clumping is likely due to the patchy co-occurrence of appropriate substrates and canopy covers. Despite substantial environmental differences between the Central Depression and the portions of the Coastal and Andean Cordilleras where *Fitzroya* is found, populations in all three regions show striking similarities in their regeneration and stand dynamics. *Fitzroya*'s longevity and at times abundant regeneration provide the biological basis for its persistence in Chile's Central Depression. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Alerce; Conifer regeneration; *Fitzroya cupressoides*; RAPD; Stand dynamics

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1. Introduction

Fitzroya cupressoides (Mol.) Johnst. (Cupressaceae, common name "alerce") is a threatened, long-lived conifer endemic to the temperate rain forests of southern Chile and adjacent portions of Argentina. It can attain a size of up to 5 m in diameter and 50 m in height, often appearing as an emergent when mixed with other species (Lara, 1991). With a lifespan greater than 3600 years (Lara and Villalba, 1993), it is one of the longest-lived tree species worldwide. Historically, *Fitzroya* was found in a variety of forest types and site conditions at elevations ranging from sea level to over 1200 m. The over-exploitation of *Fitzroya*, owing to the beauty and decay-resistance of its wood, has left extensive areas degraded and has significantly reduced its original abundance. In addition, many former *Fitzroya* forests have been intentionally burned and converted to agricultural land. *Fitzroya* re-establishment on harvested sites, as well as on most burned sites, has been scarce or nonexistent. Because of these threats, in 1975 *Fitzroya* was listed on Appendix I of the Convention on International Trade in Endangered Species (CITES), which reduced harvesting pressure on the species by banning its commercial international trade. In 1976, the Chilean government declared every living *Fitzroya* a "national monument", which provided in-country protection against further harvesting. More recently, the World Conservation Union, IUCN, has listed *Fitzroya* as endangered on their *Red List of Threatened Plants* (Oldfield et al., 1998).

In Chile, *Fitzroya* occurs in the Coastal Cordillera from ca. latitude $39°50'$ to $42°35'$, and in the Andean Cordillera from ca. $41°$ to $43°30'$. It was once abundant in Chile's Central Depression (which lies between the two Cordilleras, south and west of Llanquihue Lake; Fig. 1) before extensive logging began there in the mid-1800s. Over the last decade, several remnant *Fitzroya* populations have been
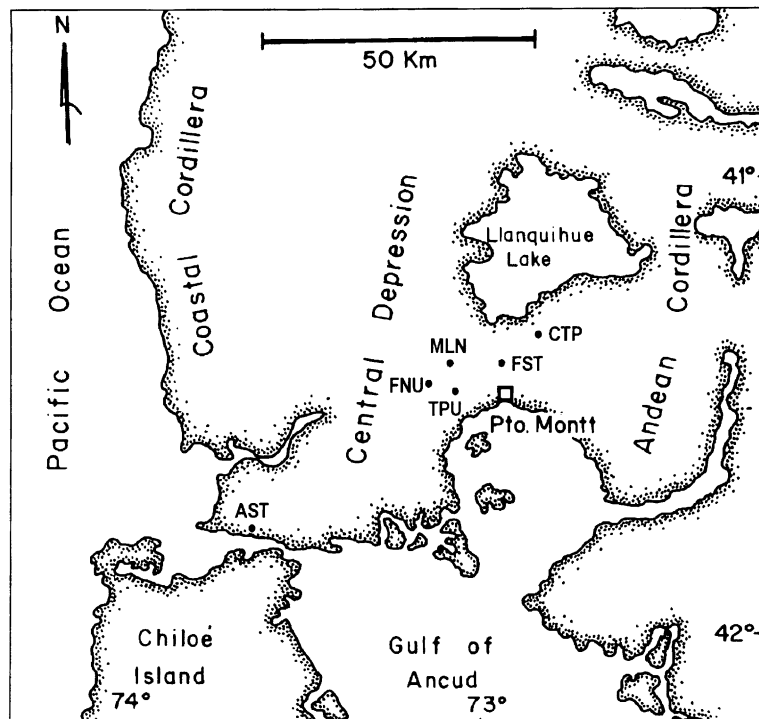

Fig. 1. Location of the *Fitzroya* study sites in southern Chile's Central Depression (AST: Astillero; FNU: Fundo Nuñez; MLN: Monumento Natural Lahuén Ñadi; TPU: Tepual; FST: Fundo Santa Teresa; CTP: Colonia Tres Puentes).

located in Chile's Central Depression, where the species was thought to have been extirpated (Veblen et al., 1976; Golte, 1996).

The current study was generated by field observations that *Fitzroya* has not re-established on much of its former habitat in the Depression, and on those sites where it currently exists, it exhibits a large amount of within- and between-site variability in seedling density. Compared to either Cordillera where *Fitzroya* occurs, the Depression has much lower rainfall, lower elevation, a longer growing season, and drastically different soils, which led us to speculate that its regeneration and stand dynamics may differ accordingly. Our objective was to determine the regeneration mode (Veblen (1992), the regeneration behavior in relation to disturbance), regeneration niche (Grubb (1977), the micro-environmental conditions under which a species becomes established), and regeneration mechanism (by seed or vegetative regeneration) of *Fitzroya* populations in the Central Depression. Given that these stands were only recently discovered, this is the first study of *Fitzroya* regeneration and stand dynamics in the Central Depression.

2. Methods

2.1. Study area

Chile's Central Depression ranges between 50 and 75 km in width, and reaches nearly 200 m in elevation in its northern extreme. From Llanquihue Lake, it gradually descends southward until reaching sea level in the Gulf of Ancud. The Depression is characterized by an oceanic cool temperate climate. 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 (300 mm per month on average).

Currently, 13 sites that support living *Fitzroya* individuals have been located in Chile's Central Depression. However, at the time this fieldwork was conducted, only nine *Fitzroya* sites were known. Six of those sites were selected for study; others were excluded owing to extreme small size or because *Fitzroya* trees were scarce and dispersed over a several hectare area, precluding the use of fix-sized plots.

The sites selected for study are referred to locally as Astillero, Colonia Tres Puentes, Fundo Nuñez, Fundo Santa Teresa, Monumento Natural Lahuén Ñadi, and Tepual. Sites lie between approximately 41°20′ and 41°45′S (Fig. 1), and elevations range from 35 to 175 m above sea level. Most stands have experienced some degree of anthropogenic disturbance, either from selective timber harvesting, cattle grazing, and/ or fire. These stands range in size from <1 to 4 ha, the larger stands often having scattered *Fitzroya* trees extending beyond their core areas.

These *Fitzroya* stands occur on acidic, shallow, poorly-drained soils referred to as *ñadis*, which are classified as Gleysols (FAO-UNESCO, 1971). They originated from Holocene volcanic ash deposited over fluvioglacial sediments. Upper horizons typically have a pH of 5.0, and are rich in organic matter (to 40%) (Besoain, 1985; Veit and Garleff, 1996). At the lower limit of the B horizon (0.4–1 m below the soil surface) one finds a 5–10 mm thick hardpan formed by iron and magnesium oxides (Grez and Carmona, 1982). This hardpan limits root development and greatly impedes drainage; stands often have pools of standing water during the winter months, yet can be very dry during the summer.

The older stands (M.N. Lahuén Ñadi, Colonia Tres Puentes, Fundo Nuñez, plot 2 of Astillero) are clearly dominated by *Fitzroya*, with *Nothofagus nitida* and *Drimys winteri* present in small amounts in the canopy. The subcanopy often includes *Tepualia stipularis*. Seedlings and saplings of *Amomyrtus luma*, *A. meli*, *D. winteri*, and *N. nitida* are common (see Fraver et al. (1999) for a floristic description of these stands). The remaining, younger stands (Tepual, Fundo Santa Teresa, plots 1 and 3 of Astillero) consist of abundant seedlings, saplings, and small trees of *Fitzroya*, often with the shrub *Baccharis magellanica* present.

2.2. Sampling design

On each of the six sites, we established at least one 20 m × 24 m permanent study plot. Given its relatively large size and varied site conditions, the Astillero site permitted the establishment of three plots (Astillero: 1, 2, and 3). We selected the 20 m × 24 m plot size as a balance between a size large enough to yield representative data, yet small enough to avoid possible

complications from forest edge effects, given the small size of several stands. All data were collected between June 1996 and February 1997. We defined trees as individuals ≥5 cm diameter at breast height (dbh = 1.4 m), saplings as individuals with a dbh < 5 cm and height > 200 cm, and seedlings as individuals < 200 cm in height. The seedling category was further broken down into two height classes, <50 and 50–200 cm.

2.3. Age-class distributions

The regeneration mode was inferred from age-class distributions, following methods of Lorimer (1985) and Veblen (1992). In each plot, we recorded by species the dbh of all living trees and snags, as well as the diameter of all cut stumps. *Fitzroya* snags and stumps are often easily identifiable by their characteristic wood and bark. We extracted increment cores from all trees at 0.3 m above the ground level and at 0.6 m when tree centers were rotten. In order to determine age structures for the younger stands, 10–20 *Fitzroya* saplings were cored (also at 0.3 m height) at each of these stands. Increment cores were mounted and sanded following the procedures of Stokes and Smiley (1968), and annual rings were counted using a stereomicroscope. When the cores did not reach the pith, the number of rings to center was estimated following the geometric procedure described by Duncan (1989). If the center was rotten, only minimum age was considered. Because the outer portions of the stumps were rotten, the year they were cut could not be determined using methods of dendrochronology.

2.4. Seedling type and abundance

We determined the regeneration mechanism—either seed or vegetative regeneration—for seedlings of the <50 cm height class. In this paper, the term *seedling* simply refers to a height class (to 200 cm height), *true seedling*, a small (<50 cm height) seedling of seed origin, and *vegling* (Parker and Donoso, 1993), a small seedling of vegetative origin. The degree of root development and size of the individuals of the 50–200 cm height class precluded determining their origin. To facilitate data collection, each study plot was divided into 10 2 m × 24 m adjacent transects. Four of the 10 transects (the first, third, sixth, and ninth) were

used to determine regeneration mechanisms of small seedlings, as well as the cover and substrate conditions (see below).

The fact that *Fitzroya* is a protected species prevented the excavation of all but a few small seedlings to determine their origin. However, without excavation, their origin could in most cases be determined by manually exploring the below-ground root system (a process facilitated by the moist, soft substrates of these sites) to ascertain if they existed independently. We recognize that natural root grafting (the fusion of roots from two or more individuals), if it occurred, would have produced overestimates of the number of veglings on a given site. However, such fusions are more common on older trees (Kozlowski and Cooley, 1961), and we assume them to be rare in small seedlings. In addition, the leaves of recently established true seedlings are paired in an opposite arrangement (as opposed to the characteristic whorl of three for this species), making their origin unmistakably from seed. In those cases where the origin could not be determined, seedlings were classified as "undetermined"; this category represented 4% of seedlings encountered. *G*-tests (Sokal and Rohlf, 1981) were applied to determine if one of these two regeneration mechanisms prevailed on each site, the null hypothesis being one of no difference.

Using the true seedlings, we characterized the regeneration niche for seedling establishment according to canopy cover and substrate. The first, third, sixth, and ninth transects were further divided into 2 m × 2 m adjacent quadrats. For each quadrat, we visually estimated the cover provided by the canopy (vegetation higher than 3 m), using one of five classes: 0–20, 21–40, 41–60, 61–80, and 81–100%. In addition, for each quadrat, we estimated the percent of surface area occupied by each of the following substrate types: leaf litter, stumps and coarse woody debris (diameters > 10 cm), humus, moss beds (including *Sphagnum* mounds), herbaceous vegetation, and small woody debris. We recorded the substrate type on which each true seedling of *Fitzroya* was found. *G*-tests (Sokal and Rohlf, 1981) were applied to determine if observed seedling density differed from that expected under the various cover classes and on the various substrate types. Expected values of seedling abundance in each cover class or substrate type were based on the relative abundance of that cover class or substrate type.

That is, abundant substrates would be expected to have proportionally more seedlings, assuming no preferences existed. Small numbers of true seedlings in various cover classes or substrate types made it necessary to pool sites in order to obtain sufficient sample sizes. Thus, true seedling data from Astillero-2, Colonia Tres Puentes, Fundo Nuñez, and Tepual were pooled for analyses of canopy cover conditions (although, Astillero-3 had abundant seedlings, the recent harvest made it inappropriate for inclusion in this analysis). Data from these same sites, including Astillero-3, were pooled for analyses of substrate conditions necessary for successful regeneration from seed.

2.5. Spatial distributions

Analysis of spatial distributions of individuals within a population can be used to determine patterns of regeneration and disturbance histories (Hubbel, 1979; Armesto et al., 1986; Gibson and Brown, 1991). We recorded to the nearest centimeter the X- and Y-coordinates for all Fitzroya seedlings, saplings, trees, and stumps on each plot, using measuring tapes aligned with each transect. Collecting data in this manner also yielded seedling, sapling, and tree densities in each plot.

For each plot, spatial patterns of all Fitzroya individuals were analyzed for random, uniform, or clumped distributions, using the function $L(t)$, a transformation of the function $K(t)$ (see Ripley, 1977; Diggle, 1983; Sterner et al., 1986). In addition, the bivariate $L_{12}(t)$ function (a transformation of $K_{12}(t)$; Lotwick and Silverman, 1982) was used to analyze the spatial interactions between (1) Fitzroya trees and small seedlings, and (2) Fitzroya trees and cut stumps. The latter analysis was done to determine if apparent clumps of trees were associated with large cut stumps, which were assumed to be of a previous cohort, based on their size and state of decomposition. We had reasoned that a positive association might suggest that the trees were the result of vegetative regeneration from root sucker sprouts of the cut stump.

Once the univariate ($L(t)$) and bivariate ($L_{12}(t)$) functions were calculated, 95% confidence limits were generated to determine if the patterns found in our observed data deviated significantly from the null hypothesis of randomness (univariate tests) or independence (bivariate tests). These confidence limits were generated by 19 Monte Carlo simulations of random point distributions, using Duncan's (1990) Spatial Analysis Programmes, which allowed pattern detection to 10 m (one-half of the shortest plot side) in our study. Univariate tests were carried out only if plots had >20 individuals within the category (seedlings, saplings, etc.) being tested. Sample size criteria were less stringent for bivariate tests, given the inherently small numbers of cut Fitzroya stumps encountered.

2.6. Genetic relationships

Results from the spatial analyses lead us to investigate the genetic relationships within clumps of Fitzroya trees ultimately found associated with Fitzroya cut stumps on two study sites. Although, clumping existed at all developmental stages (seedlings, saplings, trees), we chose to only investigate the genetic relatedness among the Fitzroya trees clumped about the large Fitzroya cut stumps to specifically test whether they were clonal sucker sprouts from those former large trees. In contrast to small seedlings, it proved impossible to trace the root systems of larger individuals; therefore, genetic analysis was the only method available for testing the occurrence of clonal structure.

Leaf material was collected from Tepual and Fundo Santa Teresa, the sites on which the association between tree clumps and cut stumps was most evident. Three clumps were analyzed at Tepual: from clump 1, five trees were sampled (age range 40–70 years); from clump 2, eight trees (74–88 years); from clump 3, five trees (43–85 years). Two clumps were sampled at Fundo Santa Teresa: from clump 1, eight trees (28–36 years); from clump 2, 12 trees (26–37 years). The largest trees (presumed to be among the oldest) within each clump were selected for sampling. Approximately 10 g of needles were collected from each tree and dried in sealed plastic bags containing silica gel (S4883 silica, Sigma Chemical Company Ltd., Fancy Road, Dorset, UK) and stored at 4 °C prior to DNA extraction. This method of sample preservation is suitable for maintaining DNA integrity (Chase and Hills, 1991). In previous work with Fitzroya, we have performed random amplified polymorphic DNA (RAPD) analyses on DNA isolated from fresh, frozen, and silica-dried samples, and have obtained

Table 1
RAPD primer sequences used to investigate genetic relationships of *Fitzroya* trees found in clumps on sites Tepual and Fundo Santa Teresa

Name	Sequence 5′–3′
OPK03	CCAGCTTAGG
OPK09	CCCTACCGAC
TAK03	CCAGCTTAGGGCAAA
TAK09	CCCTACCGACTTGAA
TAK18	CCTAGTCGAGCCTAA

identical profiles from all three sample types (results not shown).

RAPD analyses were performed on leaf material to determine if individuals found within clumps were clones. RAPD has proven to be a valuable technique for detecting vegetative regeneration in ex situ populations (Allnutt et al., 1998) and has been successfully used to identify vegetative regeneration in natural stands of *Pinus pumila* (Tani et al., 1998). The DNA isolation methods, RAPD reactions, and data analyses follow those of Allnutt et al. (1999), differing only in the RAPD primers: here we used two 10-mers (OPK03 and OPK09; Operon Technologies, Alameda, CA), and three 15-mers (TAK03, TAK09, and TAK18) primers designed specifically for this study (see Table 1 for sequences). The purpose here was simply to evaluate the genetic relatedness of clumped trees; a more detailed study of genetic variation of this species throughout its range is presented in Allnutt et al. (1999).

3. Results and discussion

3.1. Age-class distributions

All stands except Fundo Nuñez showed single-cohort age-class distributions of *Fitzroya* (Fig. 2), indicating that the populations became established in one wave of regeneration that likely followed a catastrophic disturbance. Thus, *Fitzroya*'s regeneration mode in the Depression can be considered "catastrophic" (Veblen, 1992). The distinct cohort structure of *Fitzroya* results from its shade intolerance: once a stand matures and the canopy closes, recruitment of new individuals drops off drastically. Evidence for such a drop-off can be seen as a general decrease in seedling densities with increasing canopy cover (Table 2). Sites Astillero-3 and Fundo Nuñez are exceptions, as follows. The age-class distribution for Astillero-3 is not shown in Fig. 2, because it consists of only two trees (ages 166 and 228 years) that were left after a harvesting operation that occurred between 1979 and 1986 (Ramírez, 1996). The numerous seedlings currently found on the site likely became established post-harvest. The two cohorts of *Fitzroya* found at Fundo Nuñez suggest two major disturbances. The first cohort consists of larger trees with an age range of 69–108 years (with dbh > 12 cm); the second consists of a more abundant group of trees and saplings with an age range of 18–46 years (with dbh < 12 cm). These young trees and saplings, as well as the abundant seedlings on the site, are the result of a

Table 2
Mean canopy cover, seedling densities, and prevalent regeneration mechanism for each of the eight *Fitzroya* sites[a]

Site	Mean canopy cover (%)	Seedlings height, 50–200 cm	Seedlings height, <50 cm		Prevalent regeneration mechanism
			True seedlings	Veglings	
M.N. Lahuén Ñadi	94.6	0	0	0	–
Colonia Tres Puentes	71.5	2	15	4	Seed[b]
Astillero-2	74.0	0	18	1	Seed[b]
Astillero-3	7.1	11	51	6	Seed[b]
Tepual	21.0	154	44	31	–
Astillero-1	7.7	444	1	89	Vegetative[b]
Fundo Nuñez	34.0	307	54	50	–
Fundo Santa Teresa	18.8	210	2	151	Vegetative[b]

[a] Seedling densities of the 50–200 cm height class were derived from univariate spatial analyses of the entire 20 m × 24 m plot; densities of the <50 cm height class were direct counts obtained from four 2 m × 24 m transects within each plot; sites ranked by increasing total density of small seedlings.

[b] Reproduction by this mechanism greater than expected by chance (*G*-tests; $P < 0.05$; d.f. = 1).
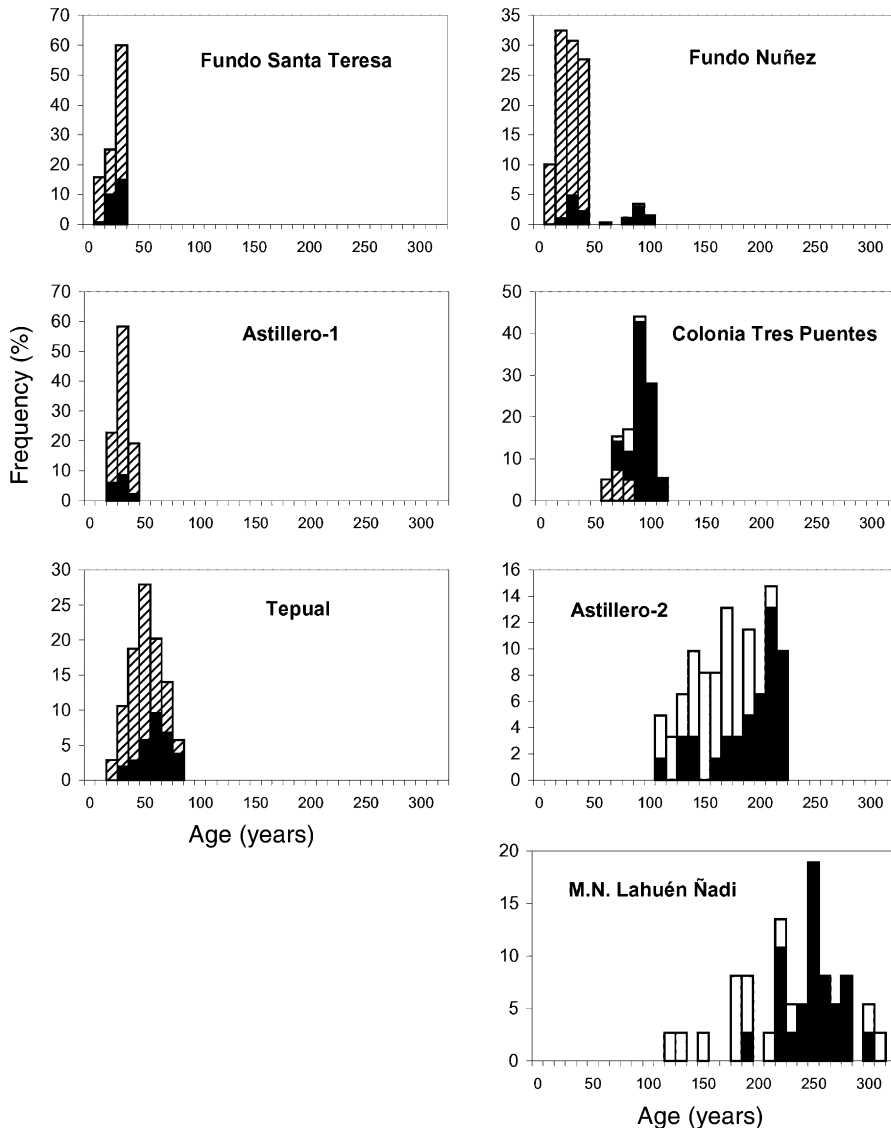
Fig. 2. Age-class distributions for seven of the eight *Fitzroya* stands under study. Astillero-3 is not shown because only two trees remain after the site was harvested. Solid bars: total tree ages; open bars: minimum ages from trees with rotten centers; stippled bars: saplings.

low-intensity fire of the early 1940s, which opened the stand enough to allow a second wave of regeneration. Evidence for this fire is based on personal communication with Alfredo Núñez (the owner), the appearance of recent fire damage on 1943 aerial photos, and growth releases in 1943 in surviving *Fitzroya* trees (Silla, 1997).

Our findings indicate that *Fitzroya*'s catastrophic regeneration mode in the Central Depression is similar to that found in both Cordilleras. However, the historic natural disturbance agents likely differed among the regions. In the Coastal Cordillera, *Fitzroya* became established after low-intensity fires (Lara et al., 1999). In the Andean Cordillera, *Fitzroya* establishment followed volcanic ash deposition, lava flows, and landslides (Lara, 1991; Donoso et al., 1993). In the Central Depression, the historic natural disturbance agent may have been fire, as abundant charcoal has been

found in pollen cores from the Central Depression (Moreno, 1998). Windthrow too may have played a role in the Central Depression, as the shallow, water-logged soils increase the likelihood of blowdowns. Windthrow from a 1994 storm is evident on two Central Depression sites; in fact, one *Fitzroya* stand adjacent to Astillero-3 was completely windthrown.

Since the colonization of the Central Depression in the mid-1800s, the disturbance regime has shifted to human-caused agents, including both frequent fire and timber harvesting. Fires used by colonists to clear land for agriculture often escaped to surrounding forests (Wilhelm, 1968). Much of this cleared land was eventually abandoned due to the low productivity of ñadi soils. Two sites (Astillero-2 and M.N. Lahuén Ñadi) survived the widespread deforestation of the Central Depression, given that their ages predate colonization of the area. The remaining sites (except Astillero-3) are most likely the result of *Fitzroya* re-establishment on previously forested sites that had been harvested and burned. Five sites (Astillero-1, Colonia Tres Puentes, Fundo Nuñez, Fundo Santa Teresa, and Tepual) clearly show signs of fire, as evidenced by aerial photographs, charred stumps, fire scars on living trees, or personal communication with the owners. Fire scars on living *Fitzroya* trees indicate that adult trees can survive low-intensity fire, a finding that has also been reported by Veblen and Ashton (1982) and Lara et al. (1999). Interestingly, Astillero-3 had abundant regeneration (3000 seedlings/ha) following a recent harvest. Although, *Fitzroya* regeneration following logging has been reported from the Coastal Cordillera (Donoso et al., 1993; Parker and Donoso, 1993), it is poor or nonexistent in the Andean Cordillera, despite seed availability from adjacent, uncut forests (Veblen et al., 1976; Lara, 1991).

3.2. Seedling type and abundance

Fitzroya regeneration was both by seed and by vegetative means. Considering all sites together, 63% of the seedlings < 50 cm in height whose origin was determined were the result of vegetative regeneration. The prevalence of vegetative regeneration, however, varied markedly among sites from Astillero-2 (6% regeneration by vegetative means) to Fundo Santa Teresa and Astillero-1 (both 99%; Table 2). Additionally, vegetative regeneration was found both as root sucker sprouts or layering, both of which have been reported for this species in the Cordilleras (Veblen and Ashton, 1982; Parker and Donoso, 1993; Lara, 1991). Two sites showed regeneration by vegetative means to be more prevalent than would be expected by chance; three sites showed regeneration by seed to be more prevalent; two sites showed no difference between the two (Table 2). Plots also differed markedly in the total number of seedlings from both size classes (<50 cm and 50–200 cm in height; Table 2).

The establishment of true seedlings was closely tied to light availability, with seedlings being more abundant in open areas, owing to *Fitzroya*'s shade intolerance. True seedling densities were much higher than expected by chance under cover classes 0–20% (observed value = 57; expected = 46.8) and 21–40% (observed = 34; expected = 22.6); they did not differ appreciably from expected under class 41–60% (observed = 23; expected = 20.2); and they were lower than expected under classes 61–80% (observed = 13; expected = 19.8) and 81–100% (observed = 4; expected = 21.7; G-test; $P < 0.005$; d.f. = 4; $n = 131$).

Results indicate that true seedling densities were much higher than expected by chance on substrates of humus (observed value = 55; expected = 33.8), moss beds (observed = 86; expected = 32.0), and stumps and coarse woody debris (observed = 27; expected = 6.7); densities were much lower than expected within leaf litter (observed = 10; expected = 62.0), herbaceous vegetation (observed = 3; expected = 26.5), and small woody debris (observed = 1; expected = 21.0; G-test; $P < 0.001$; d.f. = 5; $n = 182$). Seed dispersal is likely similar overall six substrate types; however, the abundant moisture of humus, moss, and coarse woody debris (in advanced states of decay) provides an ideal seed bed, where *Fitzroya* seedlings can survive the often dry summer months. *Fitzroya* regeneration on moss beds and fallen logs has been reported from the Andean and Coastal Cordilleras (Lara, 1991; Parker and Donoso, 1993). Further, stumps and coarse woody debris provide an elevated position, allowing seedlings increased access to light and decreased competition from herbaceous vegetation (Donoso et al., 1993). In contrast, *Fitzroya* seedlings are much less likely to be found within leaf litter (where the small radical cannot reach mineral

soil), herbaceous vegetation (where competition is high), or small woody debris (where light intensity may be insufficient).

3.3. Spatial distributions and genetic relationships

While recording data for the univariate spatial analyses, true seedlings and veglings were not differentiated. Therefore, in order to treat the two regeneration mechanisms separately, it was necessary to separate the sites into those in which the primary regeneration mechanism was by seed (Astillero-2, Astillero-3, and Colonia Tres Puentes) and by vegetative regeneration (Astillero-1 and Fundo Santa Teresa). The remaining sites could not be used in the spatial analysis of small seedlings.

True seedlings were found to be clumped at scales ranging from 4 to 10 m depending on the site, while veglings were clumped to 10 m on all sites tested (Table 3). Likewise, significant clumping of saplings was found at all scales on three of the four sites that

yielded adequate sample sizes; however, one site showed clumping only to 7 m (Table 3). Clumping of trees was found on all sites, although the scale at which clumping existed was quite variable from site to site (Table 3).

Microsite patchiness—the *co-occurrence* of appropriate substrates and canopy covers, as determined from analyses above—might explain the clumping of seedlings and saplings at the scales found here. Similarly, Gibson and Brown (1991) and Barker (1992) found clumping in the seedlings of the conifers *Lagarostrobos franklinii* and *Phyllocladus aspleniifolius* at comparable scales, and attributed this pattern to the size of appropriate microsites for regeneration by seed.

One might expect the spatial pattern of juveniles to be more clumped than those of adult trees, as clumps become thinned by mortality over time (see Sterner et al., 1986; Veblen, 1992). However, adult trees were clumped at scales similar to those of seedlings and saplings. This result is confounded by the fact that even the oldest *Fitzroya* found (316 years) may still be

Table 3
Results of univariate spatial analyses ($L(t)$) of true seedlings, veglings, saplings, and trees of *Fitzroya* on sites with >20 individuals in either group

Group	Site[a]	n[b]	Distance (t) (m)[c]																			
			1		2		3		4		5		6		7		8		9		10	
True seedlings	AST-3	132	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	CTP	25	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	–	–	–	–
	AST-2	21	C	C	C	C	C	C	C	C	–	–	–	–	–	–	–	–	–	–	–	–
Veglings	FST	260	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	AST-1	444	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Saplings	FST	105	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	AST-1	136	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	FNU	684	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	TPU	72	C	C	C	C	C	C	C	C	C	C	C	C	C	C	–	–	–	–	–	–
Trees	FST	50	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	AST-1	34	C	C	C	–	–	–	–	–	–	–	–	C	C	C	C	C	C	C	C	C
	TPU	47	C	C	C	C	C	C	C	C	C	C	C	–	–	–	–	–	–	–	–	–
	FNU	53	–	–	–	–	C	C	C	C	C	C	C	C	C	C	C	co	C	C	C	C
	CTP	86	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	AST-2	61	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	MLN	37	–	–	–	–	–	–	–	–	–	C	C	C	C	C	C	C	C	C	C	C

[a] AST: Astillero; FNU: Fundo Nuñez; MLN: Monumento Natural Lahuén Ñadi; TPU: Tepual; FST: Fundo Santa Teresa; CTP: Colonia Tres Puentes.
[b] Number of individuals.
[c] Statistical significance at the 95% level: (C) clumped patterns; (–) random spatial patterns.

Table 4
Results of bivariate spatial analysis ($L_{12}(t)$) of *Fitzroya* seedlings (either true seedlings or veglings) and trees, as well as trees and stumps

Group	Site[a]	n[b]	Distance (t) (m)[c]																			
				1		2		3		4		5		6		7		8		9		10
True seedlings/trees	AST-2	21/61	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	CTP	25/86	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	A
Veglings/trees	AST-1	444/34	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
	FST	260/50	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
Trees/stumps	FST	50/7	–	–	–	–	–	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
	TPU	47/8	A	A	A	–	–	–	–	A	A	A	A	A	A	A	A	A	–	–	–	–

[a] AST: Astillero; TPU: Tepual; FST: Fundo Santa Teresa; CTP: Colonia Tres Puentes.
[b] Number of individuals.
[c] Statistical significance at the 95% level: (A) associated patterns; (–) unassociated patterns.

considered relatively young, given the potential longevity of this species. Spatial patterns of these adults may very well change over the coming centuries due to mortality.

Bivariate spatial analyses revealed that true seedlings and trees on Astillero-2 and Colonia Tres Puentes were distributed independently from each other (i.e. no association). Astillero-3 was excluded from this analysis due to the recent harvest (see above). The fact that true seedlings were not associated with living mature trees simply reflects *Fitzroya*'s intolerance of shade, as revealed in our canopy cover analysis. Not surprisingly, veglings and trees on Astillero-1 and Fundo Santa Teresa were strongly aggregated at all scales (Table 4), suggesting vigorous sprouting of young trees both by layering and root sucker sprouting.

Fundo Santa Teresa and Tepual had *Fitzroya* cut stumps substantially larger than the diameters of the current living cohort of *Fitzroya* trees, and it appeared in the field that these trees were clumped around the cut stumps. This apparent clumping was confirmed with bivariate spatial analyses: Fundo Santa Teresa showed clumping of trees beyond 3 m from the stumps, and Tepual showed clumping to 1.5 m and then again between 4 and 8 m from the stumps (Table 4).

Given the positive association of *Fitzroya* stumps and clumps of living *Fitzroya* trees on these two sites, we had assumed that the current cohorts had arisen as sucker sprouts from cut stumps of the previous cohort. The RAPD analysis, however, revealed that trees within clumps were not clones. A total of 20 polymorphic bands were scored from which pairwise distances were calculated for all 38 samples (each individual gave a unique RAPD band profile). Without exception, polymorphic RAPD bands were observed within each clump of *Fitzroya* trees, strongly suggesting their origin from seed.

We suggest that the clumping of trees of seed origin at Fundo Santa Teresa and Tepual resulted from the patchiness of suitable microsites that existed following the stand-devastating disturbances, such as harvesting or intense fires, that gave rise to these stands. After such disturbances, these microsites were re-colonized by *Fitzroya* seed, now seen as clumps of single-cohort trees currently on each site. Disturbances such as intense fires would have killed any *Fitzroya* tissue existing at that time, thereby prevented immediate re-colonization by vegetative means. Intense fires, however, may have promoted re-colonization by *Fitzroya* seed by exposing mineral soil and removing competing vegetation. Once the stands were established, regeneration would have continued, both by seed and vegetative means. In contrast, low-intensity fires would have been followed immediately by both regeneration mechanisms. For example, Veblen and Ashton (1982) report sucker sprouting from *Fitzroya* trees that occasionally survived low-intensity fires.

4. Conclusions

Earlier authors interpreted the lack of *Fitzroya* regeneration under its own canopy or in clear-cut areas as regeneration failure of this species (see Veblen et al. (1976) and Veblen and Ashton (1982) for discussion).

More recent research has demonstrated adequate regeneration of *Fitzroya* in the Coastal and Andean Cordilleras given the appropriate site conditions (Veblen and Ashton, 1982; Lara, 1991; Donoso et al., 1993; Parker and Donoso, 1993; Lara et al., 1999). The results of this current research corroborate these findings for the Central Depression *Fitzroya* populations, demonstrating that under certain conditions, *Fitzroya* regeneration can be extremely abundant.

This is the first detailed study of *Fitzroya* regeneration in the Central Depression of southern Chile. Despite the substantial environmental differences between the Depression and both Cordilleras, *Fitzroya* populations in all three regions show striking similarities in their regeneration mode, niche, and mechanism. Our results indicate that the regeneration mode can be considered catastrophic, in that regeneration follows stand-devastating disturbances, such as fire. The regeneration niche for true seedlings is one of open canopies (<40% cover) and substrates of humus, moss beds, stumps and coarse woody debris. The regeneration mechanism includes both seed and vegetative means (root sucker sprouting and layering). Overall, vegetative regeneration was more prevalent than regeneration from seed. *Fitzroya*'s longevity and at times abundant regeneration provide the biological basis for its persistence in Chile's Central Depression. Nevertheless, its persistence there will no doubt depend on its continued protection and the availability of suitable sites for re-establishment.

Acknowledgements

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