Regeneration patterns and persistence of the fog-dependent Fray Jorge forest in semiarid Chile during the past two centuries

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Abstract

The persistence of rainforest patches at Fray Jorge National Park (FJNP) in semiarid Chile (30°40′S), a region receiving approximately 147 mm of annual rainfall, has been a source of concern among forest managers. These forests are likely dependent on water inputs from oceanic fog and their persistence seems uncertain in the face of climate change. Here, we assessed tree radial growth and establishment during the last two centuries and their relation to trends in climate and canopy disturbance. Such evaluation is critical to understanding the dynamics of these semiarid ecosystems in response to climate change. We analyzed forest structure of six forest patches (0.2–22 ha) in FJNP based on sampling within 0.1 ha permanent plots. For the main canopy species, the endemic *Aextoxicon punctatum* (Aextoxicaceae), we used tree-ring analysis to assess establishment periods, tree ages, growing trends and their relation to El Niño Southern Oscillation (ENSO), rainfall, and disturbance. The population dynamics of *A. punctatum* can be described by a continuous regeneration mode. Regeneration of *A. punctatum* was sensitive to different canopy structures. Growth release patterns suggest the absence of large scale human impact. Radial growth and establishment of *A. punctatum* were weakly correlated with rainfall and ENSO. If water limits forests patch persistence, patches are likely dependent on the combination of fog and rain water inputs. Forest patches have regenerated continuously for at least 250 years, despite large fluctuations in rainfall driven by ENSO and a regional decline in rainfall during the last century. Because of the positive influence on fog interception, forest structure should be preserved under any future climate scenario. Future research in FJNP should prioritize quantifying the long-term trends of fog water deposition on forests patches. Fog modeling is crucial for understanding the interplay among physical drivers of water inputs under climate change.

Keywords: Chile, climate change, dendroecology, disturbance regimes, fog-dependent rainforest, fog, fragmented forest, Fray Jorge, relict forest, tree regeneration dynamics

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Introduction

Isolated patches of temperate rainforest are found on the summits of coastal mountains in semiarid Chile (30°40′S), about 1000 km north of their continuous geographic range along the western margin of southern South America (37°–43°S). These forest patches are likely dependent on fog water inputs (Kummerow, 1966; del-Val et al., 2006) in a region receiving only 147 mm of annual rainfall and subjected to strong interannual rainfall variability driven by El Niño Southern Oscillation (ENSO) (Aceituno, 1992; Trenberth, 1997). The conservation status of these temperate rainforest patches, presently protected within Fray Jorge National Park (FJNP), has raised concern among forest managers in the face of future climate change and human impact (Squeo et al., 2004). Such concerns reflect general scientific uncertainty about the effects of long-term climatic trends on terrestrial ecosystems (Shugart, 1998). Fog or cloud-dependent forests have been described in tropical, subtropical and semiarid regions of the world (Hursh & Pereira, 1953; Juvik & Nullet, 1995; Hutley et al., 1997; Liu et al., 2004; Hildebrandt, 2005; Hildebrandt & Eltahir, 2006), and these may be especially sensitive to the effects of changes in hydrological variables that regulate tree regeneration and long-term survival. Possible consequences of climatic disruption of these semi-arid forests include biodiversity loss (Pounds et al., 1999), altitudinal shifts in species ranges (Sperling et al., 2004) and possibly forest loss due to increasing fragmentation and edge effects (Foster, 2001).

The forests of FJNP became separated and fragmented from the main range of coastal rainforests by climatic drying during the Quaternary (Villagrán et al., 2004). This process of aridization segmented the distributional range of rainforests, leaving scattered and isolated remnants in the northernmost limit of their main range, in the semiarid region (Villagrán et al., 2004). Forest patches in FJNP likely have a strong dependence on coastal fogs, which may double the effective precipitation and affect forest patch structure and the spatial pattern of tree regeneration and mortality (del-Val et al., 2006). Changes in fog frequency due to changes in sea-surface temperature or the height of the inversion (Cereceda et al., 2002), land-use practices (Nair et al., 2003) or changes in forest structure that may affect fog capture (e.g. Hildebrandt & Eltahir, 2006) could also have consequences for tree growth and recruitment patterns.

Remnant forest patches in FJNP have been subjected to strong, inter-annual fluctuations in rainfall associated with ENSO during the past millennia (Maldonado & Villagrán, 2002). In addition, a drying trend has occurred in the last century in central Chile (Quinn &

Neal, 1983; Le Quesne et al., 2006). Both climatic fluctuations due to ENSO or current rainfall patterns could also affect tree growth, recruitment and patch persistence. Alternatively, if the amount of fog water intercepted by trees is sufficient (i.e. it equals or exceeds their hydrological requirements), then rainfall variations would be expected to have more limited influence on tree growth and regeneration.

Here, we assessed patterns of tree establishment relative to recent changes in rainfall and the response of tree regeneration to anthropogenic (i.e. cutting or burning) or natural disturbance. We used tree-ring analysis to examine the regeneration dynamics and radial growth patterns of the dominant tree species A. punctatum (only member of the endemic family Aextoxicaeae) for the past 200 years, with the following specific goals: (1) to describe the current and past trends in the regeneration of the dominant canopy tree as an indication of forest patch persistence, (2) to develop a tree-ring chronology for A. punctatum, (3) to assess the main components of the canopy disturbance regime, and (4) to assess whether canopy disturbance and regeneration patterns of A. punctatum have been affected by recent climate trends. Finally, we discuss the importance of fog in delivering water to these forests in the context of climate change.

Materials and methods

Study area

The study was conducted in forest patches located between 400 and 600 m elevation on the coastal mountains of the semiarid region of Chile, within FJNP (FJNP, 30°40′S, 71°30′W, Fig. 1). The park was created in 1941 to protect fragments of evergreen temperate rainforest, dominated by A. punctatum. These forest patches represent the northernmost extension of southern temperate rainforests, which have a continuous distribution about 1000 km to the south (37°–43°S), with a rainfall regime exceeding 2000 mm yr^{-1} (Smith-Ramirez et al., 2005). In FJNP, A. punctatum-dominated forests are found on coastal summits influenced by oceanic fog (Fig. 1) and are surrounded by a matrix of xerophytic vegetation. Floristically, forest patches are characterized by the dominance of A. punctatum in the canopy, and the presence of the trees Myrceugenia correaefolia (Myrtaceae), Drimys winteri (Winteraceae), and Rhaphithamnus spinosus (Verbenaceae), without the presence of the sclerophyllous vegetation typical of central Chile (Villagrán et al., 2004). The patches include a species-rich assemblage of epiphytic ferns (i.e. Polypodium feillei, several Hymeophyllaceae) and woody vines (i.e. Sarmienta repens, Mitaria coccinea, Griselinia racemosa)
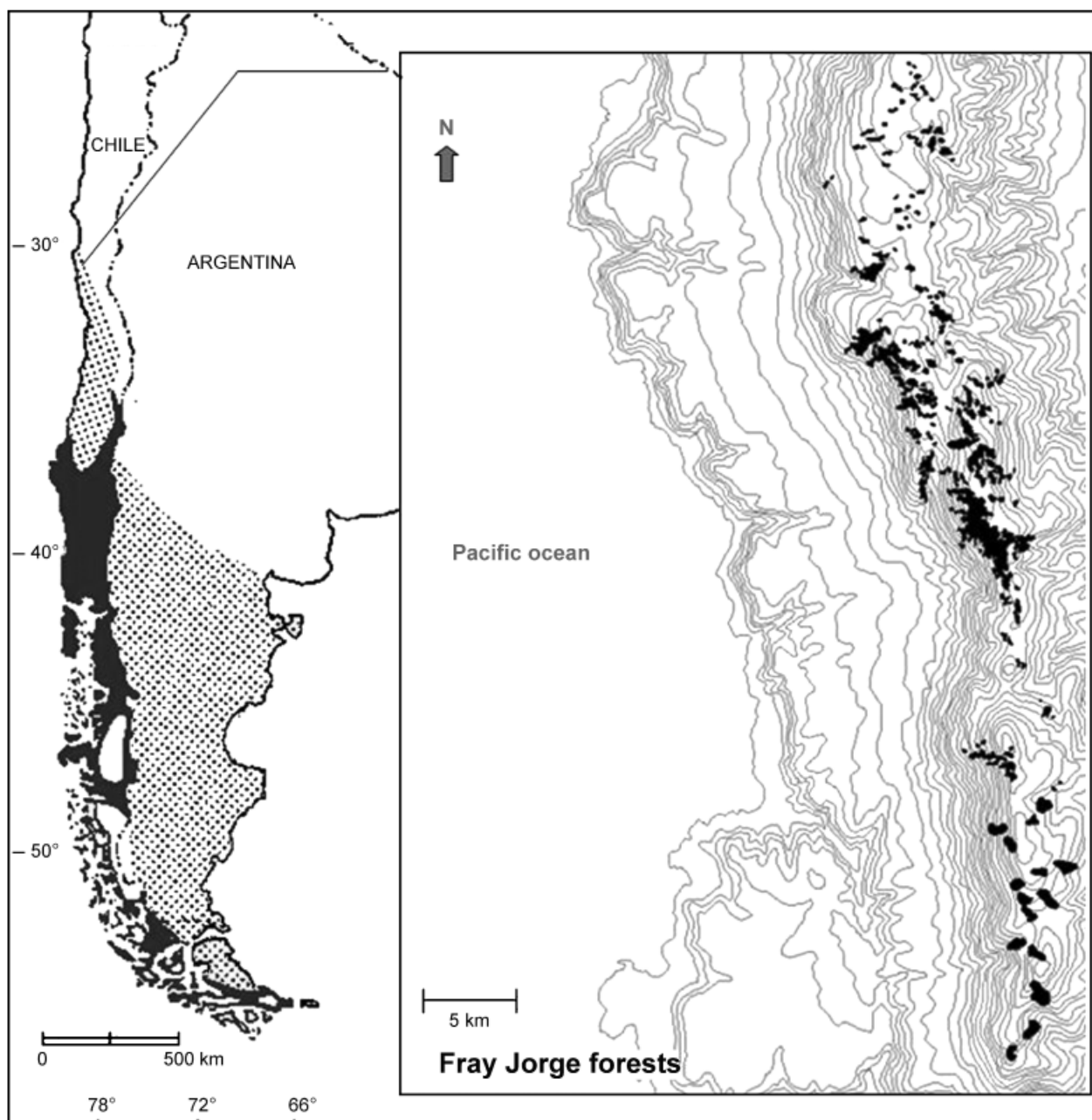
Fig. 1 Study site and overview of the Fray Jorge landscape showing the mosaic of forest patches (dark spots) on a coastal mountaintop of semiarid Chile (right side). Topographic lines of equal elevation (every 50 m) are shown. Forest patches are found above 500 m. The main distribution of southern temperate rain forests (dark shading) and semiarid ecosystems (stippled) in southern South America are shown on the left side.

which are shared with southern temperate rain forests (Villagrán et al., 2004).

The predominant climate is mediterranean-arid, with hot and dry summers and cool winters (Di Castri & Hajek, 1976). Mean annual precipitation is 147 mm, most of which occurs (>90% of total) between June and August (austral winter), with large interannual variation in rainfall (CV = 81%, $N = 21$ years) which has been associated with ENSO events (López-Cortés & López, 2004). Fog drip is spatially and temporally variable within patches (del-Val et al., 2006). Fog supplements water inputs to forest patches by an estimated 500–850 mm (Kummerow, 1966) or up to 200 mm yr^{-1} (del-Val et al., 2006). Fog deposition is a result of

stratocumulus cloud formation over huge areas in the South Pacific, that advance toward the west coast of South America (Cereceda *et al.*, 2002) and are intercepted by the vegetation on coastal mountains. The presence of fog is probably associated with the offshore cold water generated by the Humboldt current and changes in the thermal inversion layer along the coast produced by strong subsidence of the South Pacific Anticyclone (Cereceda & Schemenauer, 1991; Cereceda *et al.*, 2002).

Forest patches (Fig. 1) on coastal mountain summits of FJNP cover an area of 86.7 ha (Squeo *et al.*, 2005), ranging in size from 0.1 to 25 ha. Six forest patches were selected for this study encompassing the entire range of patch sizes in the landscape (Table 1). These are the same patches sampled by del-Val *et al.* (2006). According to locals, some forest patches were disturbed by selective logging of *D. winteri* and occasional grazing by cattle, brought in from lower grazing lands, until 1943 (Muñoz & Pisano, 1947). Fires may have affected some forest patches in the 17th and 19th centuries; limited agriculture was concentrated in the southern part of the park and at lower elevations, and it may have led to clearing of some patches (Fuentes & Torres, 1991). The intensity and spatial and temporal extent of these disturbances, however, is unknown.

Patch structure

We used one permanently marked plot ($50\,\text{m} \times 20\,\text{m}$ each) in the interior of each selected forest patch to characterize forest structure. Evidence of human impact (stumps or fire scars) was recorded if present (Table 1). We marked, identified to species and recorded the diameters at 1.3 m above the base (dbh) of all trees (stems $>1.3\,\text{m}$ height and $\text{dbh} > 5\,\text{cm}$) inside each permanent plot. Trees were classified as alive (healthy), some branches dead, or standing dead (snags). The presence of vegetative stems (i.e. derived from sprouting) was also recorded. Because vertical stratification is relevant to fog interception by the forest patches (Weathers, 1999), we assessed the heterogeneity of vertical canopy structure using the Berger–Parker diversity index (d) (Magurran, 2004). This index is based on tree-crown positions and provides a measure of stratification and canopy heterogeneity though the proportional importance of the most abundant canopy class: $1/d = 1/(N_{max}/N)$ where N_{max} is the number of individuals in the most abundant canopy class and N is the total number of individuals. A high value of the index reflects greater vertical heterogeneity. Canopy classes of each tree inside the plots were recorded as: emergent, above canopy height; dominant, in the canopy tier; intermediate, directly under the canopy with

Table 1 Characterization and summary of structural parameters for all tree species found in six forest patches sampled in FJNP, Chile

Patch name	Forest patch area (ha)	Altitude	Slope (%)	Aspect	Berger–Parker index	Total number of seedlings and saplings ($N\,\text{m}^{-2} \pm \text{SE}$)	Juveniles trees ($N\,\text{m}^{-2} \pm \text{SE}$)	Evidence of recent human impact
F1	0.2	566	11	W	3.33	3.5 ± 1.9	3.4 ± 1.0	Cutting of the woody vine *Griselinia*, fire in surrounding matrix
F2	0.3	529	1	W	3.28	2.0 ± 0.8	7.7 ± 1.5	Cutting of the woody vine *Griselinia*, fire in surrounding matrix
F3	2.0	495	35	SE	3.75	16.7 ± 9.2	3.1 ± 0.8	None
F4	3.9	566	10	SW	3.95	1.0 ± 0.4	3.9 ± 0.8	Tourist trail, fire in surrounding matrix
F5	14.2	635	42	SW	3.61	14.1 ± 5.6	6.9 ± 1.4	None
F6	22.0	639	38	SW	3.75	9.3 ± 2.9	7.8 ± 2.1	None

The Berger–Parker Index indicates vertical stratification.
SE, standard error of the mean; FJNP, Fray Jorge National Park.

light only from above; and subcanopy, permanently shaded.

Along three linear transects inside each selected patch, separated from one another by 10–25 m depending on patch size, we distributed seven sampling points 20 m apart. At each sampling point, tree seedlings and saplings (stems <1.3 m height) were counted and identified to species within a 1 m^2 quadrat, while juveniles (stems >1.3 m in height but dbh <5 cm) were counted and identified within a circular plot of 2 m radii (del-Val *et al.*, 2006).

Dendrochronology

We used the empirical dbh distribution of *A. punctatum* trees (stems >5 cm dbh) in the permanent plots to randomly and uniformly select a sample of 30 *A. punctatum* trees for coring, across the dbh size classes (of 10 cm each) represented within each patch. Additional cores were taken from the largest trees in each patch (nine per patch). Cores were taken at about 1.3 m from the base of the stem and processed following standard dendrochronological techniques (Stokes & Smiley, 1968). Samples with <25% of the stem radii intact or without distinguishable tree-rings were discarded ($n = 38$); a total of 196 cores (from 180 trees) were suitable for tree-ring analysis.

Minimum tree ages were estimated by counting tree-rings of each core. Tree rings were visually cross-dated assigning a calendar year to each tree ring, based on the date of the latest ring (Stokes & Smiley, 1968). We assigned to each tree-ring the date in which radial growth started (Schulman, 1956). When the pith was missing (23% of all cores), the number of rings to the pith was estimated using a geometrical method (Duncan, 1989). After visual cross-dating, radial growth increments were measured to the nearest 0.01 mm with an increment-measuring device and recorded in a computer. The computer program COFECHA (Holmes, 1983) was used to detect errors in measurements and cross dating. We used the best crossdated trees ($N = 28$ trees) from different patches to produce the tree-ring chronology. Ring-width records for each tree were standardized and then averaged with the other trees to produce a mean chronology (Fritts, 1976). Standardization involves fitting the observed ring width series to a curve or a straight line and computing an index of the observed ring widths divided by the expected value. This reduces variances among cores and transforms ring widths into dimensionless index values. Thus, standardization permits computation of average tree-ring chronology without the average being dominated solely by the faster growing trees with large ring widths (Fritts, 1976; Villalba & Veblen, 1997). The standard chronology was done with the ARSTAN program (Cook, 1985).

For all complete cores of *A. punctatum*, we defined the year when the tree became established in the forest, corrected by age to coring height (1.3 m), which was estimated as 10 years from dbh–age linear regression. All trees >100 years old ($n = 45$ overall) were examined for releases of radial growth. Releases were taken as evidence of canopy opening (presumably due to disturbance) and used to infer patch dynamics (Lorimer & Frelich, 1989). We defined a major growth release as an increase >100% in the average radial growth of the current year relative to the previous year, which lasted for at least 15 years afterwards. A moderate release was defined as an increase of >50% in average radial growth between subsequent years, lasting for at least 15 years afterwards (Lorimer & Frelich, 1989). The sustained release criterion of 15 subsequent years was used to eliminate short-term climatic pulses and gradual ring-width changes due to tree aging, bole geometry, and long-term climate shifts (Lorimer & Frelich, 1989).

Statistical analyses

Tree regeneration (seedling and sapling mean densities) was compared among forest patches using analysis of variance. Age–dbh regression analysis for *A. punctatum* was performed to evaluate if dbh distributions were indicative of age structures. Dbh distributions for all species pooled and for *A. punctatum* populations were tested with models often assumed to represent a continuously regenerating population (Veblen, 1992). Dbh distributions in each patch were described using a nonlinear least-squares fit of a power function: $y = ax^b$, where y is stem density, x represents dbh class, a and b are parameters. Spearman's rank correlations were used to assess the relationship between patch size, Berger–Parker index and forest patch structure variables. Structural variables considered were vegetative reproduction (percent sprouting stems), snag (percent standing dead trees) and potential tree regeneration (density of seedlings and saplings, plus juveniles).

We evaluated the effect of climate variables on the ring-width index (RWI) of *A. punctatum* (standard chronology) using a correlation function analysis (Fritts, 1976). RWI was correlated against monthly rainfall data over the period 1900–2002 using rainfall data from La Serena (29°54′S, 71°12′W), the nearest meteorological station to FJNP and the longest climate record in the area (1870–2000). We also analyzed the relationship between RWI and the Southern Oscillation index (SOI; Aceituno, 1992; Trenberth, 1997; data from the Bureau of Meteorology, Australian Government).

We examined a sequence of months starting with the previous growing season (September–May previous year of growth) and ending in May of the year in which the ring was formed (i.e. at the end of the current growing season). Limited, discontinuous historical fog data based on field observations of daily frequency of stratus clouds (fog) since 1970 were available for FJNP from CONAF and Dirección Metereológica (Chile).

Cross-correlations were used to check for dependencies between climate (annual values of fog, precipitation, SOI), RWI, releases and the recruitment time series. Data analysis involved the use of a 'prewhitening' procedure to remove autocorrelation before cross-correlation analysis (Box & Jenkins, 1976). First, the time series were analyzed for the presence of autoregressive structure and, if present, its order was determined by examining the partial autocorrelation functions (Box & Jenkins, 1976). We used a maximum likelihood fitting of autoregressive-moving average models to estimate an appropriate model for each time series. Residual series were computed by subtracting the observed values from those predicted by the autoregressive model. After removal of autocorrelations, cross-correlations using different time lags were computed between the residual time series to see how they related in time. All statistical analyses were conducted in R STATISTICAL software (R-Development-Core-Team, 2005).

Results

Patch structure and current regeneration

Mean seedling and sapling density (stems <1.3 m height) ranged from 1 to 16.7 ind. m^{-2} and mean juvenniles densities (stems >1.3 m height but <5 cm dbh) ranged from 3.1 to 7.8 ind. m^{-2} (Table 1). No differences were detected in mean seedling density ($F_{(5, 12)} = 2.48$, $P = 0.09$) and mean juvenile density ($F_{(5, 12)} = 2.13$, $P = 0.13$) among patches. Forest patches varied in terms of their vertical canopy structure. Lower values of the Berger–Parker index were found in smaller patches Fl and F2, and larger values in both intermediate and large patches, indicating higher vertical heterogeneity in the latter (Table 1). However, no significant correlation was found between patch size and the Berger–Parker index ($P = 0.32$).

The canopy of all six forest patches was dominated by *A. punctatum*, except for patches F1 and F5, which were co-dominated by *M. correifolia* and *A. punctatum* or by *D. winteri* and *A. punctatum*, respectively (Table 2). *R. spinosus* and *Azara microphylla,* were occasionally ($<7\%$) represented in the canopy of the forest patches. *M. correifolia* and *D. winteri* had their greatest representation in patches F1 and patch F5, respectively (Table 2).

Pooling all tree species, seedling densities were uncorrelated with patch size or with the Berger–Parker index (Table 3). Seedlings of *M. correifolia* declined with increases in patch size (Table 3). The relative density of *A. punctatum* seedlings and juveniles also varied significantly among patches ($F_{(5, 12)} = 15.71$, $P<0.01$) increasing with patch area (Tables 3 and 4). *Myrceugenia* had the highest relative density of juveniles in smaller patches, accounting for $>50\%$ of juveniles, and decreasing with patch size (Table 3). In contrast, relative density of *A. punctatum* juveniles and of *A. punctatum* trees was positively correlated with the Berger–Parker index (Table 3). Total densities of juveniles and trees,

Table 2 Relative density ($N\%$) and relative basal area (BA%) for all live stems (>5 cm dbh), snags (standing dead trees) and vegetative stems (% of all stems in the plot, horizontal and/or vertical, originating from other stems) in six forest patches (F1–F6) in FJNP, Chile

| | | Patches | | | | | | | | | | | |
| | | F1 | | F2 | | F3 | | F4 | | F5 | | F6 | |
	Tree species	N%	BA%	N%	BA%	N%	BA%	N%	BA%	N%	BA%	N%	BA%
Live stems	*Aextoxicon punctatum*	10.6	49.0	33.6	75.7	45.6	71.3	86.9	93.9	15.2	46.4	77.4	88.8
	Drimys winteri	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.8	77.3	52.0	19.4	10.8
	Myrceugenia correifolia	89.0	50.8	51.3	21.6	38.9	24.6	5.6	4.0	0.8	0.3	0.4	0.2
	Other species*	0.4	0.2	15.1	2.7	15.4	4.2	4.7	1.3	6.6	1.3	2.8	0.3
Proportion of vegetative stems		65.9	65.8	68.0	86.0	61.7	80.5	44.6	59.8	21.1	36.9	41.9	57.1
Snags		16.6	23.0	11.1	19.4	6.0	9.0	5.6	1.3	9.1	1.2	13.4	9.0
Totals		2270	49.4	1520	61.6	1490	46.7	3590	90.4	3610	125.1	2520	102.6

Azara michropylla, Raphithamnus spinosum, Griselinia racemosa (vine), and *Adenopeltis serrata* (understory shrub).
Totals represent accumulated stem density (N ha^{-1}) and basal area (m^2 ha^{-1}) per patch.
SE, standard error; FJNP, Fray Jorge National Park.

Table 3 Spearman rank correlations (r_s) for the relationship of patch area and Berger–Parker index ($n = 6$) with other demographic and structural variables analysed

	Patch area			Berger–Parker index		
	r_s	$t_{(N-2)}$	P-level	r_s	$t_{(N-2)}$	P-level
Total seedlings density	0.03	0.06	ns	−0.03	−0.06	ns
Total juveniles density	0.77	2.42	ns	−0.03	−0.06	ns
Total snag density	0.14	0.29	ns	−0.03	−0.06	ns
Total vegetative stems density	−0.14	−0.29	ns	0.37	0.80	ns
Relative seedling density						
Aextoxicon punctatum	0.94	5.66	***	0.66	1.74	ns
Drimys winteri	0.88	3.71	**	0.46	1.02	ns
Myrceugenia correifolia	−0.83	−2.96	**	−0.71	−2.04	ns
Relative juvenile density						
Aextoxicon punctatum	0.77	2.42	ns	0.89	3.82	**
Drimys winteri	0.94	5.57	***	0.58	1.41	ns
Myrceugenia correifolia	−0.94	−5.66	***	−0.66	−1.74	ns
Relative snag density						
Aextoxicon punctatum	−0.54	−1.29	ns	−0.54	−1.29	ns
Relative vegetative stems density						
Aextoxicon punctatum	−0.26	−0.53	ns	−0.94	−5.66	***

***$P < 0.01$.
**$P < 0.05$.
ns, not significant.

Table 4 Regeneration of *Aextoxicon punctatum* (N m^{-2} ± standard error) observed in six forest patches (F1–F6) in FJNP, Chile, and regression parameters (*a* and *b*, see 'Materials and methods') estimated for the power function fitted to stem density by dbh class in each patch (all trees and *A. punctatum* trees, dbh > 5 cm)

	Aextoxicon punctatum regeneration		Regression parameters for dbh distributions							
			All trees				*Aextoxicon punctatum* trees			
Patch	Seedlings/saplings	Juveniles	*a*	P-level	*b*	P-level	*a*	P-level	*b*	P-level
F1	0.05 ± 0.05	0.05 ± 0.05	199 5000.0	***	−3.4	***	272.6	ns	−1.28	***
F2	0.05 ± 0.05	0.24 ± 0.20	35 400.0	***	−2.2	***	300.6	ns	−1.10	***
F3	1.0 ± 0.54	0.52 ± 0.21	357300.0	***	−3.0	***	16 098.3	***	−2.21	***
F4	0.14 ± 0.08	1.71 ± 0.74	24 0800.0	**	−2.5	***	147800.0	**	−2.42	***
F5	3.0 ± 0.86	1.57 ± 0.65	857949.6	**	−3.0	***	71 321.3	**	−2.81	***
F6	2.62 ± 0.87	2.38 ± 1.88	22 576.7	***	−1.9	***	7140.0	**	−1.61	***

***$P < 0.01$.
**$P < 0.05$.
ns, not significant; FJNP, Fray Jorge National Park.

analyzed separately, were uncorrelated with patch vertical structure (Table 3).

Dbh-distributions in all six patches fitted the power function model (Table 4). Accordingly, there were trees in most size classes describing a continuously regenerating forest community. Dbh distributions of *A. punctatum* followed this general tendency except in patches F1 and F2, which had nonsignificant fit for power function parameter *a* (Table 4). In all the patches, larger dbh classes (> 60 cm dbh, maximum dbh = 155 cm) were dominated by *A. punctatum*. In contrast, *M. correifolia* was characterized by numerous small stems in smaller patches Fl, F2 and F3 (dbh < 45 cm). *D. winteri* dominated the canopy of patch F5 (Table 2), with a population of small and medium size trees (dbh < 45 cm, Fig. 2).

A high proportion of all sampled stems (46%, $n = 1504$) in all patches were derived from vegetative
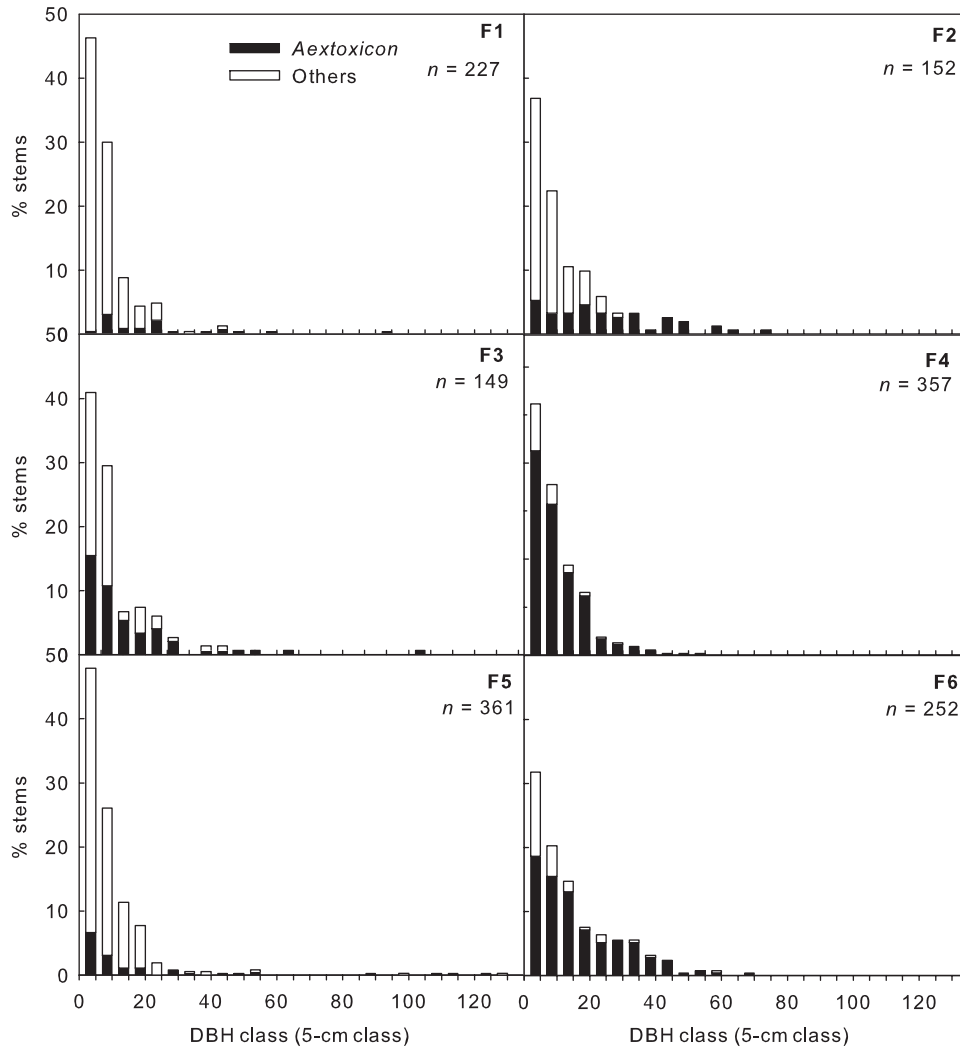
Fig. 2 Diameter (dbh) class distribution of main canopy trees (dbh >5 cm) in six forest patches in Fray Jorge National Park. Data for *Aextoxicon punctatum* only (dark bars) and for all other tree species pooled (white bars) are shown.

sprouting. Furthermore, 52% of all *A. punctatum* stems sampled ($n = 705$) were of vegetative origin. Vegetative sprouting represented >60% of total stem density and >68% of total basal area in the smaller patches (F1–F3; Table 2). The relative density of vegetative stems of *A. punctatum* in each patch was negatively correlated with the Berger–Parker index (Table 3). Snags comprised >15% of stems and 19% of the total basal area in the smaller patches F1 and F2 while large patches generally had <10% of stems and basal area as snags. Large patches had greater numbers of smaller size, dead trees under the canopy than smaller patches, where all dead trees were found along edges (Table 2).

Age structure and growth patterns of A. punctatum

Across all patches, minimum ages estimated for *A. punctatum* trees ranged from 25 to 213 years ($n = 196$).

With the exception of F4, *A. punctatum* had similar age structures in the patches, (Kruskal–Wallis $H = 9.39$, $P = 0.06$, F4 excluded from analysis; Fig. 3). For *A. punctatum*, we found a significant linear regression between age and dbh [$\ln(\text{age}) = 0.6435 \times \ln(\text{dbh}) + 2.2478$, $r^2 = 0.77$, $F_{(1, 130)} = 434.4$, $P < 0.01$]. Thus, for *A. punctatum* in FJNP dbh distributions were roughly indicative of age structures.

Regeneration history of adult *A. punctatum* stems (>5 cm dbh) across all patches showed tree recruitment in all 5-year intervals between 1860 and 1965 (Fig. 4a). Recruitment peaks were recorded during 1925–1930 and 1950–1960 especially in F4 (Figs 3 and 4a). The youngest tree dated was recruited in 1977, thus trees <5 cm represent relatively frequent recruitment during the last two decades. Based on age–dbh regressions, most large individuals of *A. punctatum* (dbh >1 m) in the forest patches were probably recruited before 1810.
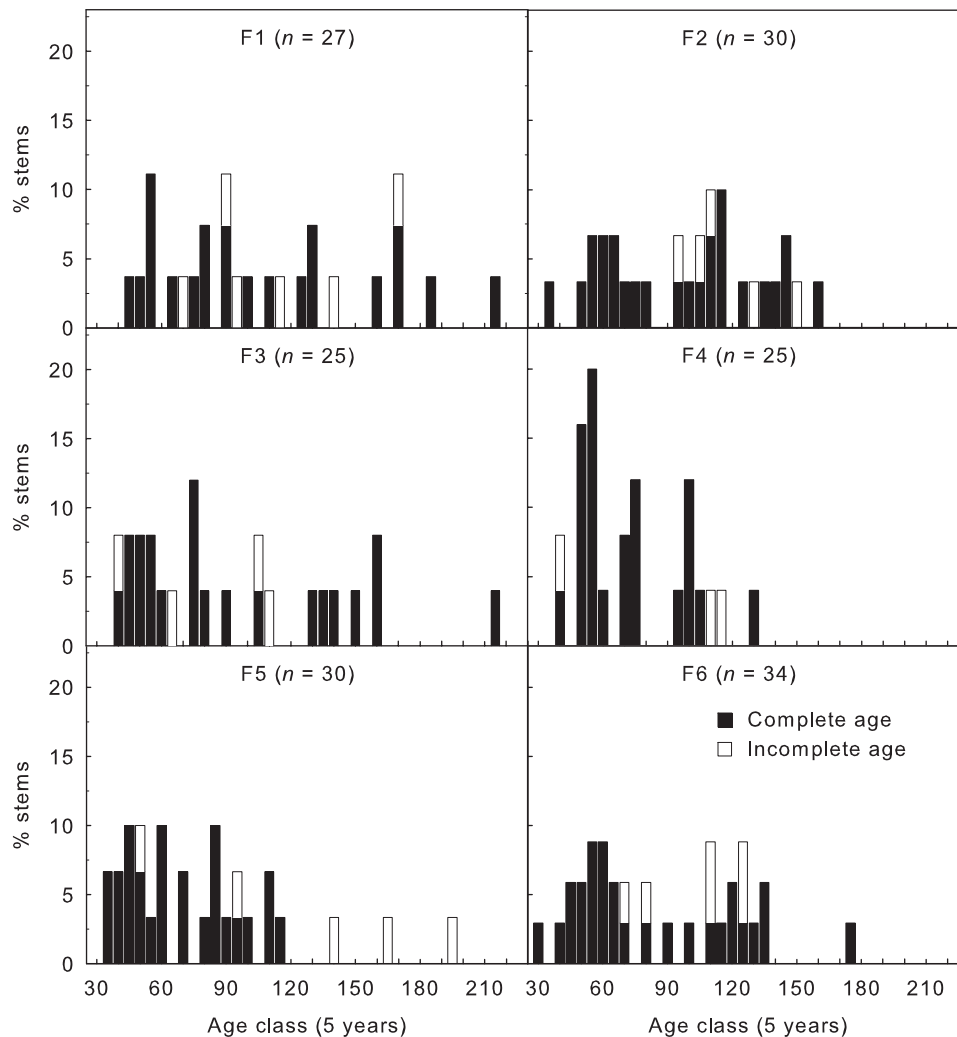
Fig. 3 Age distribution (stems >5 cm dbh) of *Aextoxicon punctatum* in six forest patches in Fray Jorge National Park. Sample sizes (complete plus incomplete cores) are given in parentheses. Patches are named as in Table 1.

The recruitment date expected for the largest tree in the sample was approximately 1760 (dbh = 155 cm), about 240 years ago.

Radial growth patterns of *A. punctatum* showed several releases from suppression that suggest local disturbance at small scale (i.e. tree falls), which opened the forest canopy, increasing the radial growth of previously suppressed trees. Trees tended to grow faster in larger patches (1.4 mm yr^{-1}, patches F3–F6) than in smaller patches (0.9 mm yr^{-1}, patches F1–F2) (Kruskal–Wallis $H = 17.3$, $P < 0.001$). Although some trees sampled produced sustained releases of >3 times than the magnitude of previous growth, moderate releases were more common than major releases (Table 5) and were present in all 5-year intervals since 1870 to the present (Fig. 4b). Releases comprising a large number of trees in the patches studied occurred during the periods

1925–1930 and 1875–1880. From 1955 to the present, the frequency of moderate releases declined relative to the previous century (Fig. 4b). Growth releases were entirely absent between 1850 and 1870, even though >10 trees covered this time period. No differences were detected in the number of releases recorded between patches (major releases Kruskal–Wallis $H = 2.6$, $P = 0.27$; moderate releases, Kruskal–Wallis $H = 4.1$, $P = 0.13$).

The tree ring chronology for *A. punctatum* covered the period from 1795 to 2002 (Fig. 4c). The chronology does not show any obvious tendencies in radial growth, except for large fluctuations around the mean in the period 1830–1915. Fluctuations decreased towards the present as sample size increased. Tree radial growth declined slightly after 1900 (linear regression, $r^2 = 0.20$, $F_{(1, 102)} = 12.73$, $P < 0.01$), a trend that became more pronounced from 1950 to the present. During this latter
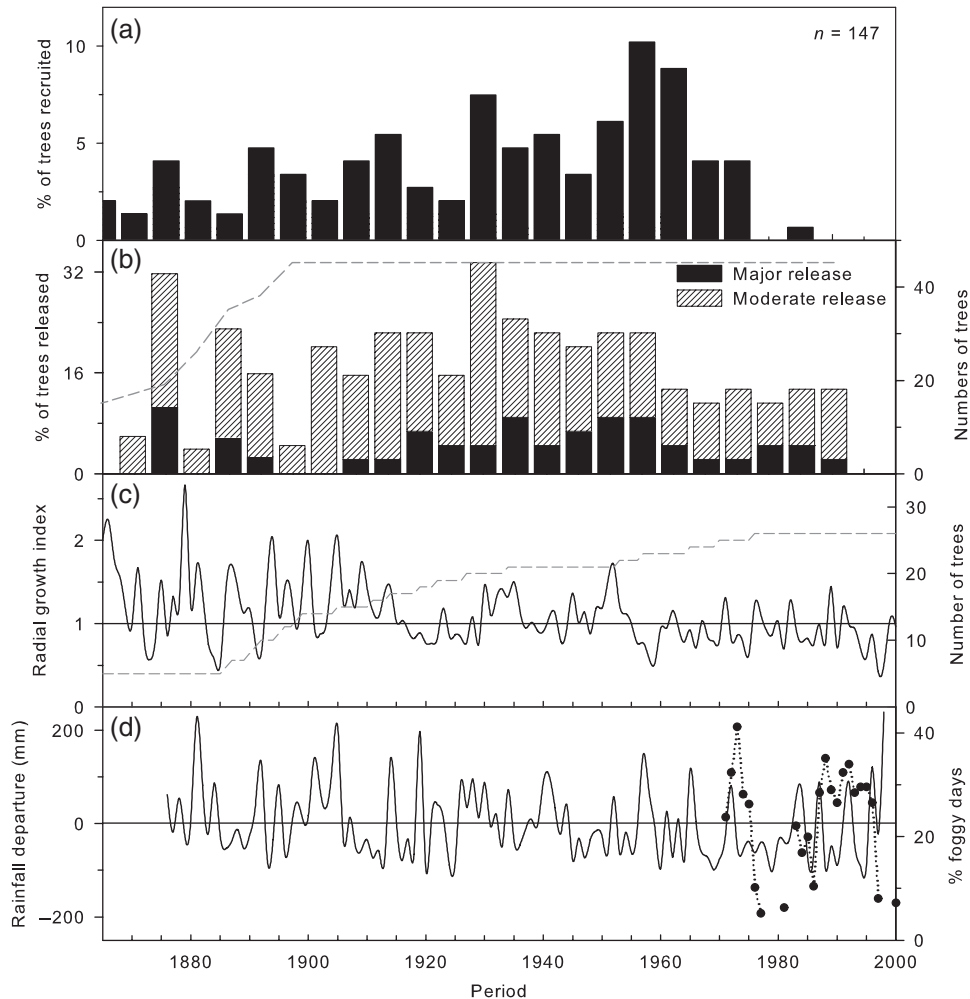
Fig. 4 (a) Recruitment frequency of *Aextoxicon punctatum* (stems >5 cm dbh) in each 5-year interval over the past 150 years in six forest patches of Fray Jorge National Park (FJNP) (pooled sample from all patches). (b) Major and moderate radial growth releases recorded per 5-year interval in 100-year-old *A. punctatum* trees in six forest patches in FJNP (samples pooled); (c) tree-ring width chronology of *A. punctatum* in FJNP (from all six patches). Continuous line represents radial growth departures from the expected mean value (horizontal line). Dashed lines in (b) and (c) represent the sample size for each 5-year period; (d) rainfall departures (mm yr^{-1}) from the mean annual rainfall calculated for instrumental records from 1876 to the present (horizontal line) in La Serena meteorological station (30°S) about 50 km north of FJNP. Points and dotted lines indicate percentage of fog days during each year, estimated by the presence/absence of low clouds in the forest area from daily records by Fray Jorge park guards.

period, tree growth was predominantly below the mean (Fig. 4c). Some depressions of growth rates (−0.5 unit below the mean, i.e. 1959, and 1997–1998) were recorded. The greatest peak in radial growth since the 1920s occurred in 1952 despite the general trend toward slower growth.

Correlations with climate

We found a weak correlation between ring width of *A. punctatum*, rainfall and SOI (Fig. 5a). A significant, positive correlation between RWI and the spring rainfall of the previous growing season (November) was

detected while a negative correlation was seen with late winter rainfall (August) of the current year of growth (Fig. 5a). We found a negative correlation between RWI and SOI of winter of the current year (July). Quantitative analysis of fog influences (Fig. 5b) was not conducted due to the lack of consistent long-term fog records but these data were plotted, as a reference, relative to RWI and rainfall (Fig. 4d). The recruitment pattern of *A. punctatum* during the past 175 years was significantly correlated with the mean accumulation of rainfall over the previous 5 years (Fig. 5c). Finally, SOI was uncorrelated with observed periods of tree recruitment and growth releases.
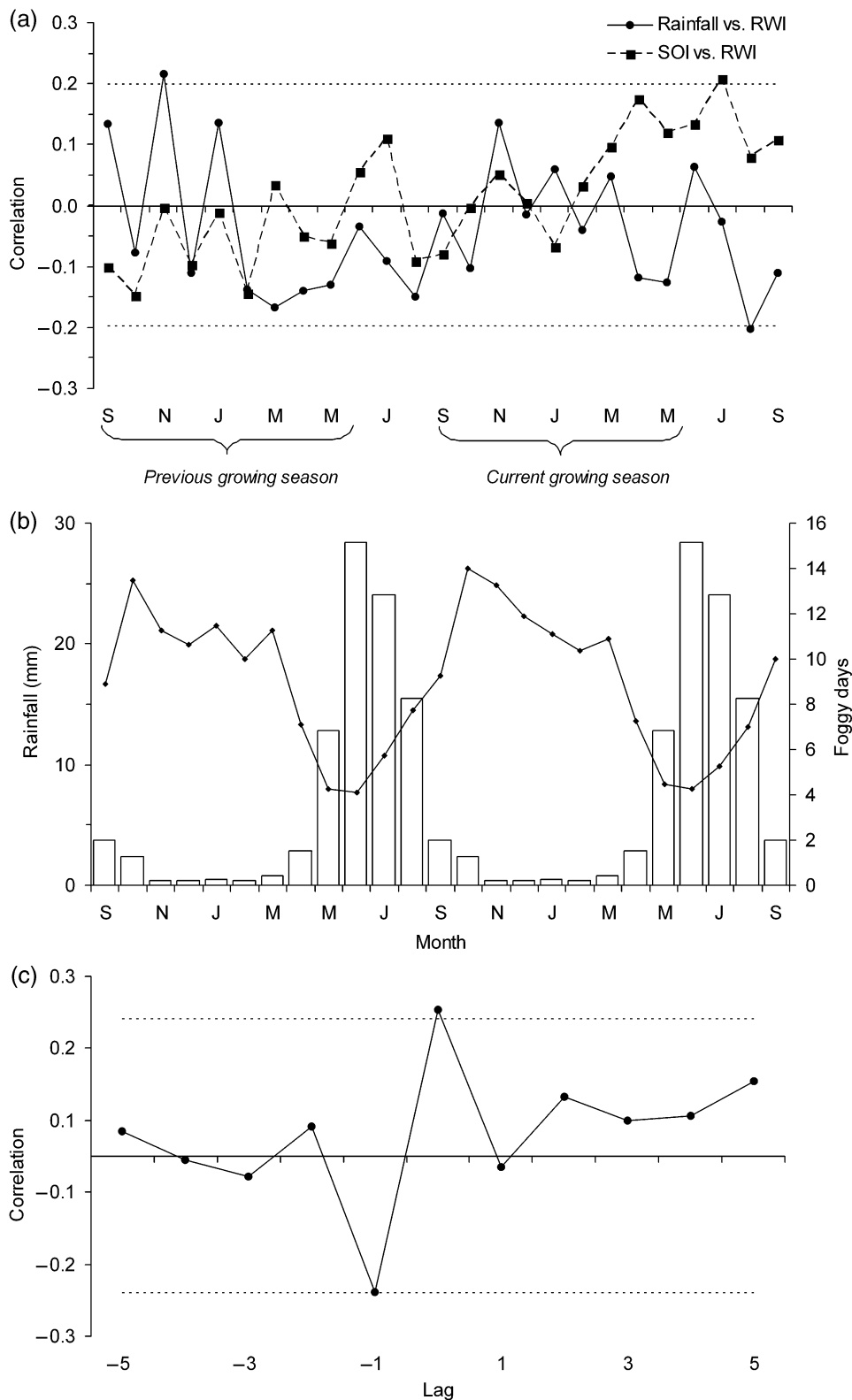
Fig. 5 (a) Correlation functions (Pearson's *r*) between current year monthly rainfall, monthly Southern Oscillation index and tree ring width of *Aextoxicon punctatum* for the past 100 years. (b) Monthly variation in rainfall (mm, open bars) and proportion number of fog days (line) as in Fig. 4d. (c) Cross-correlation function between the tree recruitment time series (total number of live trees recruited per year between 1875 and 1980) and total rainfall accumulated during the previous 5 years. Simple prewhitening of all time series was done before computation (see 'Materials & methods'). Dotted lines in (a) and (c) represent the 95% confidence intervals for the correlations.

Discussion

Regeneration and patch structure

A clear pattern emerges from the analysis of tree regeneration. Seedling densities of *A. punctatum* were higher in the larger and vertically more structured patches (meaning higher heterogeneity in canopy classes). The same pattern held for other tree species, with the exception of *M. correifolia,* which had a greater density in smaller patches. Smaller patches in FJNP have greater susceptibility to soil and litter desiccation due to increased edge effects (Barbosa, 2005) and more herbivore abundance (del-Val *et al.*, 2007), which may be responsible for the lower seedling and juvenile densities. The importance of vegetative reproduction as a form of persistence under stress conditions has been reported in a diversity of ecosystems (Bond & Midgley, 2001), including semiarid, fog-dependent forests (Hildebrandt, 2005). In the case of *A. punctatum*, natural regeneration coupled with high vegetative reproduction is likely to ensure its persistence in medium and large forest patches (>2 ha). Persistence of *A. punctatum* is less certain in small patches (<2 ha) because of limited seedlings densities (Table 3, Fig. 2).

The relative success of seedlings in reaching juvenile size appears to be dependent on forest patch structure. Juvenile densities of *A. punctatum* showed no relationship to patch size, but heterogeneity of vertical structure was significantly correlated with juvenile densities as well as with vegetative reproduction of *A. punctatum* (Table 3). Because vertical structures such as trunks, limbs, branches and leaves are responsible for fog interception and water drip within the forest (Kerfoot, 1968; Dawson, 1998; Weathers *et al.*, 2001), patch structure may play an important role in increasing the potential for fog capture. *A. punctatum* is the dominant canopy species, and thus is likely responsible for much of the current fog interception. To the extent that this system depends on water inputs from fog, regeneration and persistence of other tree species in forest patches may be dependent on *A. punctatum*'s continued successful regeneration and growth. These results point to the importance of forest structure in recruitment and suggest an important role of fog and water drip, whose delivery amounts are dependent on vertical structure (Weathers, 1999; Weathers *et al.*, 2001).

Disturbance and regeneration of A. punctatum

A continuous regeneration mode best represents the pattern of recruitment of *A. punctatum* in forest patches of FJNP over the past 250 years. Despite some exceptions, such as less establishment in small patches during the past 50 years, most forest patches showed fairly continuous tree regeneration, with some moderately marked recruitment pulses (especially in F4). This regeneration pattern has resulted in an uneven-aged canopy of *A. punctatum*. Such pattern of recruitment has not been previously reported in *A. punctatum*-dominated coastal forests. A single-cohort population was reported in another fog forest on Santa Ines hill (31°S), about 200 km south of Fray Jorge, suggesting that *A. punctatum* became established there following stand-disrupting disturbance (Le Quesne *et al.*, 1999). Whether such disturbance was climatic or human related is unknown. Such large disturbances, affecting entire patches, were not apparent in the FJNP forest. Fire scars were absent from trees in all patches. Small canopy disturbances are shown by frequent moderate growth releases in 1875–1880 and 1920–1930, as suggested by coincident release chronologies of various trees (Fig. 4b). Although Lorimer & Frelich (1989) caution against interpretation of releases in environments with prolonged dry seasons, the lack of strong correlation of RWI with rainfall (discussed below) supports the idea that these are disturbance-related releases. Moderate releases imply the occurrence of circumscribed, low-intensity disturbances, such as small canopy openings arising from individual tree falls (Lorimer & Frelich, 1989). Such disturbances were present in all 5-year intervals from 1870 to present suggesting a relatively unstable canopy, which may be related to shallow soils and root systems. The predominance of low-intensity disturbance suggests that individual tree-falls could happen at any time as a consequence of windstorms, especially on steep slopes. There was no evidence of significant canopy disturbance in the last 50 years, suggesting either a less windy climate or a reduction of spatially discrete human impact after the creation of FJNP in 1941.

Climate influences on tree regeneration and radial growth

The tree ring chronology for *A. punctatum* (Table 5) showed strong interannual fluctuations of tree growth, which may reflect variable local environmental conditions and past disturbance (Fritts, 1976). Only a small proportion of the variation in tree ring widths was explained by differences in annual rainfall ($r = 0.2$, Fig. 5a). Similar results have been reported for another tree species (*Prosopis chilensis*) characteristic of semiarid vegetation near our study area (Holmgren *et al.*, 2006). In the case of *Prosopis*, lack of correlation with rainfall is related to its deep tap root dependence on deep soil water sources. These results, however, are in contrast

Table 5 Radial growth patterns of *Aextoxicon punctatum* trees in six forest patches in FJNP

Chronology statistics	
Sample size (number of trees)	28
Period	1795–2002
Mean radial growth (mm/year) ± SE	0.94 ± 0.24
Average mean sensitivity	0.31
Standard deviation	0.35
First order autocorrelation	0.29
Mean correlation between trees	0.33
Dendroecological statistics	
Sample size (number of trees)	45
Maximum radial growth (mm/year) [95% percentile]	15.3 [3.15]
Maximum sustained release*	9.4
Moderate release frequency (releases/100 years)†	2.2
Major release frequency (releases/100 years)†	0.7

Releases defined after Lorimer & Frelich (1989).
*Average growth rate for the 15 years period following the release event, divided by the growth rate for the 15 years prior to release.
†Release frequencies for the past 100 years were calculated averaging the number of growth releases recorded for each tree and dividing by tree age.
SE, standard error of the mean; FJNP, Fray Jorge National Park.

with the high correlations between radial growth and rainfall (Pearson > 0.4) observed in *Austrocedrus chilensis,* further south in the central Chilean Andes (Le Quesne *et al.*, 2006), where annual rainfall (ca. $400 \, mm \, yr^{-1}$) is greater than in our study area and oceanic fog is absent. At FJNP, foggy days are more numerous when rainfall is minimal (Fig. 5b), and fog inputs as well as water drip in 2003–2004 was greatest in the austral spring and summer (Barbosa, 2005; del-Val *et al.*, 2006).

Because rain contributes only a portion of the tree water budget in Fray Jorge forest, then fluctuations in rainfall are unlikely to be the major determinants of tree growth, although the seasonality of water inputs is likely to be important as well (Weathers, 1999). While reduced radial growth of *A. punctatum* in the last century might result from the gradual decrease in average annual rainfall reported for semiarid Chile (Quinn & Neal, 1983; Le Quesne *et al.*, 2006), only late winter rainfall in the previous year was positively correlated with RWI over the last 100 years (Fig. 5a). Because of the high likelihood that *A. punctatum* growth is water limited in this region (del-Val *et al.*, 2006), and not light-limited as it is farther south (Donoso *et al.*, 1999), slower tree growth in the past 50 years may be

the result of a decrease in late winter rain or total water input (i.e. rainfall plus fog). The lack of long-term fog data does not allow us to assess fog influences on long-term patterns of tree growth relative to other phenomena such as lagged responses to habitat fragmentation (Vellend *et al.*, 2006). However, the forest structure and recruitment data presented here and earlier work in these forests (Barbosa, 2005; del-Val *et al.*, 2006) suggests that a relationship with fog variability could be present.

Climate in semiarid Chile is connected to SOI patterns. Rainy years are generally associated with the positive phase of ENSO cycles (Montecinos & Aceituno, 2003) and changes in cloud cover and height are also possible due to a higher subsidence inversion during strong ENSO events (Rutllant *et al.*, 2003). Some decreases in radial-growth (i.e. 1997 and 1845) could be partially explained by the influence of strong ENSO events (Ortlieb, 1994; Montecinos & Aceituno, 2003). However, we currently do not know how this variability in SOI may affect coastal fog input to coastal mountain forests. The recruitment pattern of *A. punctatum* was positively correlated with the accumulation of rainfall during the previous 5 years (Fig. 5c), and RWI was positively related to the previous year's late winter rainfall (Fig. 5a). However, neither of these patterns are sufficient for us to be able to detect the effects of reductions in rainfall on tree recruitment, such as characteristic drought conditions of La Niña episodes during the negative phase of ENSO (Montecinos & Aceituno, 2003; Fig. 4a). Clearly there is a need o understand the role of ENSO cycles in fluctuations of fog and rain because it might influence the recruitment patterns of *A. punctatum* on subdecadal time scales (e.g. observed gaps in the recruitment patterns of *A. punctatum* over the last century, Fig. 4a). A combined index of fog plus rain could be useful in understanding growth patterns of *A. punctatum* in this semiarid region.

Decrease in winter rainfall (60–80% of current amount) has been predicted in the study area for year 2100 (DGF & CONAMA, 2006), but changes in fog frequency and fog base over time are uncertain (e.g. Pounds *et al.*, 1999; Nair *et al.*, 2003; Sperling *et al.*, 2004). Fog frequency may vary in response to changes in sea temperature, the height of the inversion layer (Cereceda & Schemenauer, 1991; Cereceda *et al.*, 2002) or wind direction. These changes in precipitation, fog frequency and water content may affect the position, size and shapes of forest patches via influences on tree growth and recruitment (del-Val *et al.*, 2006). Because these water sources may respond to different climatic drivers, it is especially important that multiple dimensions of climate change be considered.

Forest persistence assessment

Overall, our findings indicate that *A. punctatum* has recruited consistently in these forest patches for at least 250 years, despite large fluctuations in rainfall driven by ENSO cycles, which have characterized this region for the past millennia (Maldonado & Villagrán, 2002). No evidence for decreased recruitment following declining rainfall (Quinn & Neal, 1983; Le Quesne *et al.*, 2006) in the last century was found in large patches, but recruitment in small patches may be more susceptible because of their propensity for drying. Although regeneration patterns of *A. punctatum* are sensitive to patch size and canopy structure, a continuous regeneration mode has prevailed over the past 150 years. Tree radial growth and establishment success of *A. punctatum* were weakly related to rainfall, but may be responsive to variability in fog input or to total fog and rain input among years. Nevertheless, the complex interplay between rain and fog water inputs and their direct bearing on tree growth patterns over long time periods still needs to be elucidated. A better understanding of how changes in climate may affect the timing and distribution of water sources and the development of models predicting fog trends will be important in assessing the ability of these forests to persist in the face of climate change. Vertical heterogeneity of patches has favorable effects on the recruitment success of *A. punctatum*, likely because of the positive influence on fog interception. Thus, preservation of forest structure may be critical to patch hydrology under any future climate scenario. In fact, complex patch structure may compensate at the landscape scale for declining long-term trends in rainfall, as long as fog capture remains high. Further research of FJNP should prioritize the maintenance of long-term records of fog and rainfall in order to make reasonable predictions about the future of the forest and tree growth patterns. Fog modeling; in particular, needs to be better incorporated in current global or regional climate models.

Acknowledgements

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