

Rain Forest Islands in the Chilean Semiarid Region: Fog-dependency, Ecosystem Persistence and Tree Regeneration

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ABSTRACT

Tree presence in semiarid ecosystems is generally constrained by insufficient annual rainfall. However, in semiarid Chile, rainforest patches dominated by *Aextoxicon punctatum* are unexpectedly found on coastal mountaintops (450–600 m) at 30°S, surrounded by a xerophytic vegetation matrix that receives only 147 mm of annual precipitation. It has been proposed that these forests persist as a result of fog-water inputs. If so, then because fog-water deposition is spatially heterogeneous and shows strong edge effects, the potential environmental gradient created by the direction of fog input should determine forest structure and tree regeneration patterns. To investigate this hypothesis, we measured fog inputs, forest structural attributes (age and size distribution, basal area, and coarse woody debris), and tree regeneration in three different habitats: the windward

edges (WE), leeward edges (LE), and the interior (center) of rainforest patches varying in area from 0.2 to 22 ha. Mean fog-water input was estimated from passive collectors over 1 year in WE and LE of patches. Tree regeneration was greater in the WE and forest interior (FI) and decreased toward the LE of patches, following a marked pattern of decline in fog inputs. Older trees and coarse woody debris were concentrated in the FI and LE of patches. Tree regeneration and patch structure appear to be largely controlled by fog-input direction and edge effects. We propose that forest patches may be slowly growing toward the incoming fog edge, while dying at the opposite edge.

Key words: *Aextoxicon punctatum*; edge effects; forest structure; tree regeneration; mortality; water limitation; Chile.

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INTRODUCTION

Trees are generally considered to be excluded from semiarid regions by insufficient rainfall (Grace 1997). For example, in the steppe–forest border of southern Patagonia, trees are replaced by shrubs when rainfall is less than 400 mm per year (Veblen

and Markgraf 1988). Worldwide, shrubs replace trees in semiarid regions when precipitation is less than 300–400 mm (Holdridge 1947). In the semiarid region of Chile (30°S), where annual precipitation (150 mm, López-Cortés and López 2004) is well below that usually associated with tree growth, temperate rainforest patches nonetheless, persist on coastal mountaintops, surrounded by a matrix of xerophytic vegetation (Squeo and others 2004). The ecological and historical factors that could explain the persistence of these isolated rainforest patches in this northern outpost have long been a subject of inquiry among botanists, ecologists, and biogeographers (Philippi 1884; Muñoz and Pisano 1947; Skottsberg 1948). Despite their improbable location, these forests bear a striking floristic similarity to Valdivian temperate rainforests found 1,000 km to the south (Villagrán and Armesto 1980), where rainfall far exceeds 2,000 mm per year.

These rainforests are dominated by the tree *Aextoxicon punctatum* (Olivillo), the only member of the endemic family Aextoxicaceae. Evergreen Olivillo forests are distributed continuously along the ocean-facing slopes and deep ravines of the Coastal mountain range from about 33–43°S, but isolated, remnant patches occur north of 33°S, on coastal mountaintops in the semiarid region, where coastal fogs are prevalent (Kummerow 1966). Within this broad latitudinal range, annual rainfall varies from 2,657 mm at the southern limit of Olivillo distribution (Isla Guafo 43°40' S) (Smith-Ramirez et al 2005), to less than 147 mm at Fray Jorge National Park (FJNP) (30°40' S) (Armesto and others 1996; López-Cortés and López 2004).

In this northern outpost, Olivillo forests consist of a mosaic of small, isolated patches found only on coastal mountaintops. A number of investigators have proposed that Olivillo trees are able to exist in a semiarid area where rainfall is insufficient for tree growth and survival by using water from frequent coastal fogs, thereby enabling the persistence of an associated rich assemblage of rainforest species (Philippi 1884; Looser 1935; Muñoz and Pisano 1947; Skottsberg 1948; Schmithusen 1956; Kummerow 1966; Villagrán and Armesto 1980).

Fog moves inland from the Pacific Ocean on westerly winds – the prevailing wind system along the west coast of southern South America since the Holocene (Heinz 1998; McCulloch and others 2000). Fog is frequent between 500- and 700-m elevation on the ocean-facing, coastal mountains of the semiarid region of Chile (Rundel and Mahu 1976; Cereceda and Schemenauer 1991; López-

Cortés and López 2004), and coincidentally Olivillo forests are restricted to this altitudinal range in this northern location. Recent experimental studies using stable isotopes indicate that Olivillo trees obtain a major part of their water from fog (P. Vidiella and T. E. Dawson unpublished data). Fog occurrence and fog water deposition are not homogeneous in the coastal landscape. Fog-water deposition depends on fog frequency, liquid water content, wind speed and direction, and most importantly, on the presence of plant surfaces capable of intercepting fog (Weathers and others 1992, 2000). To be a source of water for plants, wind-driven fog droplets must be intercepted by the tree canopy (for example, Azevedo and Morgan 1974; Dawson 1998; Schemenauer and Cereceda 1994). “Captured” fog-water is then redistributed by the stems and leaves of trees. Although fog-water can be taken up by leaves (Burgess and Dawson 2004), it also drips from the canopy and is routed to the forest floor via throughfall and stemflow (Hutley and others 1997; Dawson 1998). In addition, fog-water deposition is spatially heterogeneous; where edges exist, it has been shown to decrease predictably from the windward (WE) to the interior of forests because of interception by trees (Beier and Gunderson 1989; Erisman and others 1997; Weathers and others 1995, 2000; 2001).

Based on the above, we hypothesized the existence of a “fog shadow” associated with distinct rainforest patches such that the windward forest edges would receive greater fog inputs that would impact a wide range of other patterns in this landscape. Because the trees in these forest patches may largely depend on fog as a water source, we propose that the forest would create a windward-to-leeward environmental gradient orientated toward the fog-input direction, and that this gradient may be one of the main factors determining patch structure as well as tree regeneration and mortality patterns within these forest patches. We tested three specific hypotheses about the correlation between fog inputs and forest patch structure in this northern outpost of temperate rainforest and predicted that (1) fog-water deposition is heterogeneous between patches and higher at the WE than at the leeward edge (LE) of forest patches; (2) tree regeneration is concentrated toward the edge of the incoming fog, whereas basal area, tree mortality, and coarse woody debris increase away from it; and (3) different tree species are distributed within forest patches in relation to their different drought tolerances.

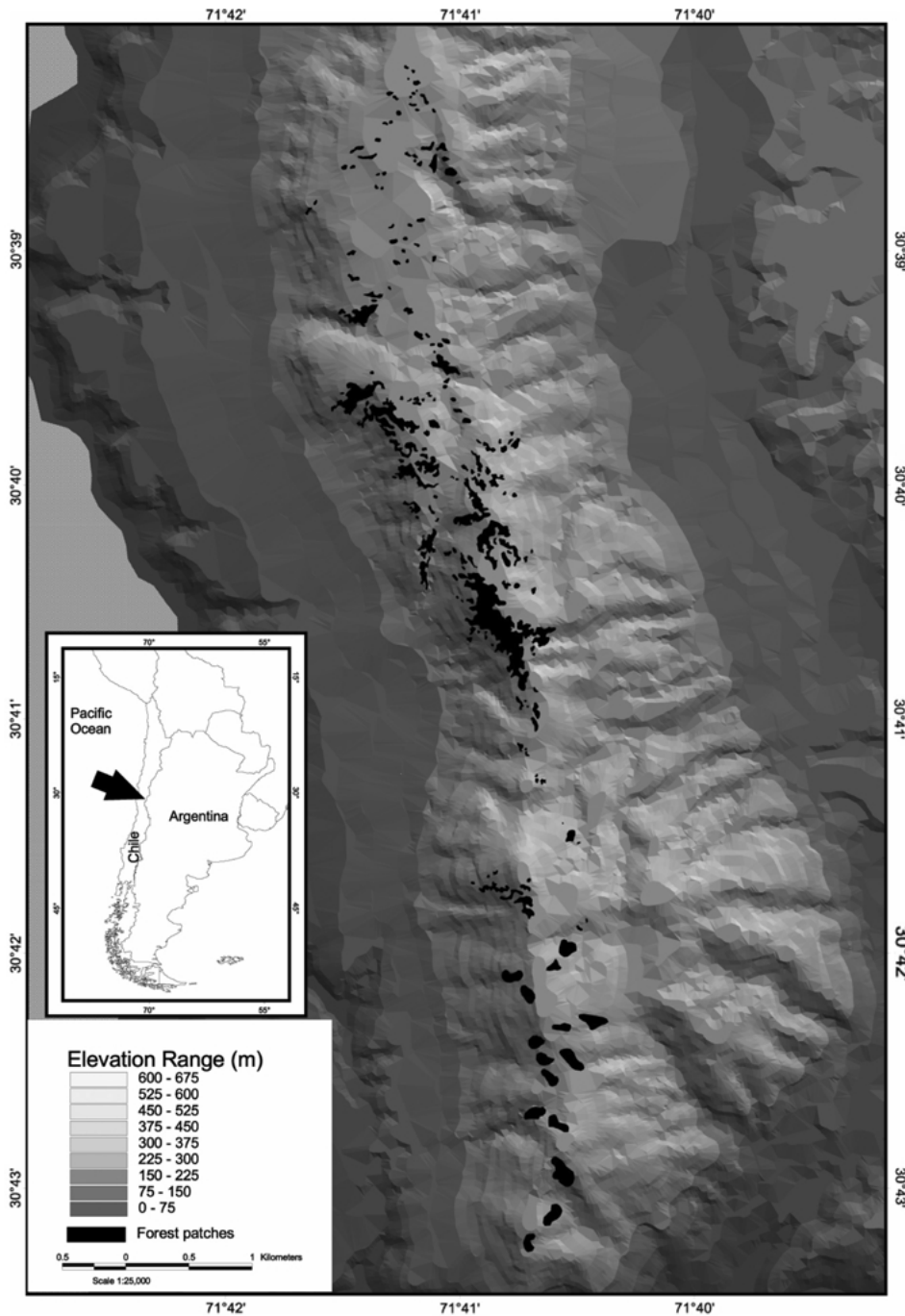


Figure 1. Location of study site showing the rainforest patch mosaic in Fray Jorge National Park. Modified from Novoa-Jerez and others (2004).

STUDY SITE

The study was carried out at Fray Jorge National Park (FJNP), (30°40’S, 71°30’W), the northernmost location of Olivillo forest. Here, a mosaic of 180 rainforest patches, ranging in size from 0.1 to 22 ha, occurs on the summits of coastal mountains (450–660 m a.s.l.) within a matrix of semiarid scrub vegetation (Novoa-Jerez and others 2004). Smaller patches tend to be located on the mountain plateau, whereas larger patches are on steeper slopes

facing the ocean, thus having a larger zone of fog influence (Figure 1). It is important to note that fog is patchy and that due to the complex topography, delivery of fog is not uniform across the landscape. In large patches, fog can follow different directions as it moves down ravines, for example. The regional climate is characterized as mediterranean-arid with hot-dry summers and cool winters (Di Castri and Hajek 1976). Mean annual temperature is 13.6°C and mean annual precipitation is 147 mm (from 21-year records, 1983 – 2003) (López-Cortés

and López 2004), falling mostly (around 95 % of annual rainfall) in the austral winter, between June and August. There is a substantial interannual variability in rainfall coefficient of variation ($CV = 81\%$), with wet pulses every 3–5 years, associated with positive phases of El Niño–Southern Oscillation (ENSO), and dry periods associated with negative phases (Jaksic 2001; Montecinos and Aceituno 2003; López-Cortés and López 2004).

In addition to Olivillo trees (*Aextoxicon punctatum*, Aextoxicaceae), the rainforest patches contain other broad-leaved evergreen trees—namely, *Myrceugenia correifolia* (Myrtaceae), *Drimys winteri* (Winteraceae), *Rhaphithamnus spinosus* (Verbenaceae), and *Azara microphylla* (Flacourtiaceae). Woody vines such as *Griselinia scandens* (Cornaceae), *Sarmienta repens* and *Mitraria coccinea* (both Gesneriaceae), and epiphytic ferns (for example, *Polypodium feullei*) are frequent components of the forest canopy (Muñoz and Pisano 1947; Villagrán and Armesto 1980; Squeo and others 2004). Understory plants are generally small herbaceous species such as *Peperomia fernandeziana*, and *P. coquimbensis* (Piperaceae), and shrubs such as *Adenopeltis serrata* (Euphorbiaceae), and *Ribes punctatum* (Saxifragaceae). In addition, tree trunks are covered by a dense coat of mosses, lichens, and liverworts, evidence of the high internal humidity of forest patches.

METHODS

In August 2003, we sampled vegetation and patch structural attributes (tree regeneration, tree age and size distribution, basal area, tree density, and coarse woody debris) in six forest patches above 500 m (0.2 – 22 ha), (Table 1) representing the heterogeneity of patch sizes found in FJNP (Squeo and others 2004). We defined the following habitats in each patch: (1) WE, mostly facing the westerly winds and therefore first to receive incoming fog; (2) forest interior (FI), located under closed canopy at the center of each patch and at least 50 m away from any edge in large patches and 15 m away in small patches; and (3) LE, opposite to the fog-receiving edge, mostly facing east. It is important to note that because of local topography (Figure 1) the wind does not always blow from west to east; hence, wind direction varies slightly with forest patch location.

Fog Inputs

To assess the relationship between fog-input direction (that is, edge effects) and structural attributes of forest patches (Figure 1), we set up

two passive fog collectors (PFC) outside five of the patches sampled for structure (Table 1). The PFC measured fog-water inputs to the WE (facing approximately west) and LE (facing approximately east) edges of each patch. Each PFC had a cylindrical capturing surface made of dark plastic mesh (shade cloth), with 5-mm square openings, to enable fog collection from all directions. The capturing surface was 50 cm in height by 15-cm in diameter and was placed 1.5 m from ground level, on top of a 15-cm-wide funnel, connected by a plastic tube to a 10-L lidded storage bucket containing mineral oil to prevent evaporation. Water volume captured was measured monthly for a period of 12 months from September 2003 to August 2004, by emptying the storage bucket at the end of each sampling period. Water captured by PFC was the sum of fog-water plus rainwater, but rainwater was restricted to a few days between June and August 2004 (see Figure 2). Fog-input data were expressed as the volume of water collected (millimeters per collector per month) converted to millimeters of precipitation equivalents by dividing the volume collected by the PFC capturing-surface area.

Tree Regeneration

In each of the six patches, we set up three parallel transects, one per habitat, oriented approximately from north to south and perpendicular to fog-input direction. Transects were separated from each other by at least 10 m in small patches, and by 25 m in larger patches. We distributed ten sampling points separated by 20 m intervals along each transect line (200 m long). At each sampling point, we determined the density and diameter of canopy trees and the abundance of saplings and seedlings. The density, basal area, and composition of canopy trees (stems more than 1.3 m in height and more than 5 cm in diameter at breast height [dbh]) was estimated using the point-centered quarter method (Cottam and Curtis 1956). At each point, we recorded the distance from the four nearest trees to the sampling point, their identities and dbh. The densities of seedlings (stems less than 1.3 m in height) and saplings (stems more than 1.3 m in height but less than 5 cm dbh) were estimated within 1-m² quadrats for seedlings and 2-m-radius circular plots for saplings. Nomenclature of species followed Marticorena and Quezada (1985).

Tree Ages

To assess the current minimum age of canopy-dominant Olivillo trees inside the patches, we col-

Table 1. Tree Species Abundance and Presence of Fog Collectors in Different Patches

Fragment size (ha)	Species	Abundance (individuals/0.1 ha)	Fog collector
0.2	<i>Aextoxicon punctatum</i>	24	Yes
	<i>Myrceugenia correifolia</i>	202	
	<i>Drimys winteri</i>	0	
	<i>Azara microphylla</i>	0	
	<i>Rhaphithamnus spinosus</i>	1	
0.3	<i>Aextoxicon punctatum</i>	51	Yes
	<i>Myrceugenia correifolia</i>	78	
	<i>Drimys winteri</i>	0	
	<i>Azara microphylla</i>	19	
	<i>Rhaphithamnus spinosus</i>	4	
2	<i>Aextoxicon punctatum</i>	68	Yes
	<i>Myrceugenia correifolia</i>	58	
	<i>Drimys winteri</i>	0	
	<i>Azara microphylla</i>	8	
	<i>Rhaphithamnus spinosus</i>	12	
3.9	<i>Aextoxicon punctatum</i>	312	Yes
	<i>Myrceugenia correifolia</i>	20	
	<i>Drimys winteri</i>	10	
	<i>Azara microphylla</i>	11	
	<i>Rhaphithamnus spinosus</i>	3	
14.2	<i>Aextoxicon punctatum</i>	55	Yes
	<i>Myrceugenia correifolia</i>	3	
	<i>Drimys winteri</i>	279	
	<i>Azara microphylla</i>	11	
	<i>Raphithamnus spinosus</i>	13	
22	<i>Aextoxicon punctatum</i>	195	No
	<i>Myrceugenia correifolia</i>	1	
	<i>Drimys winteri</i>	49	
	<i>Azara microphylla</i>	7	
	<i>Rhaphithamnus spinosus</i>	0	

lected increment cores at breast height (1.3 m) from 98 individuals. The largest trees found along the three transects sampled for forest structure were selected for coring. At least three trees were sampled in each transect. Cores were processed according to Stokes and Smiley (1968). When tree cores did not reach the center, whenever possible the number of missing rings was extrapolated following the geometric procedure described by Duncan (1989). Incomplete ages are reported for trees with rotten centers (13% of the total). Cores with less than 25% of the radii present were discarded ($n = 21$).

Coarse Woody Debris

We determined the spatial distribution of coarse woody debris (CWD) (snags or logs more than 10 cm in diameter)—an indicator of tree mortality patterns and disturbance legacies in temperate rainforest landscapes (Carmona and others 2002)—from a 2-m-wide transect that followed the main fog-input

direction (that is, from WE toward LE) in each patch. Transect lines were extended 50 m on each side beyond the edge of the forest patches to assess the presence of woody remains outside the present patch area. Data are expressed as the volume of CWD present within transects and in each habitat type. Habitat types for CWD were defined as follows: WE, from 50 m outside the patch edge to the beginning of the area of continuous canopy inside the patch; FI, completely under continuous canopy; and LE, from where the continuous canopy ended extending 50 m outside the back edge.

STATISTICAL ANALYSES

The volume of water captured by PFC during 2003–2004 was separated by position (WE and LE) for each forest patch ($n = 5$ patches). Volume of water collected in the PFC was converted to milliliters of water (that is, precipitation equivalents) and analyzed by a nested analysis of variance (ANOVA),

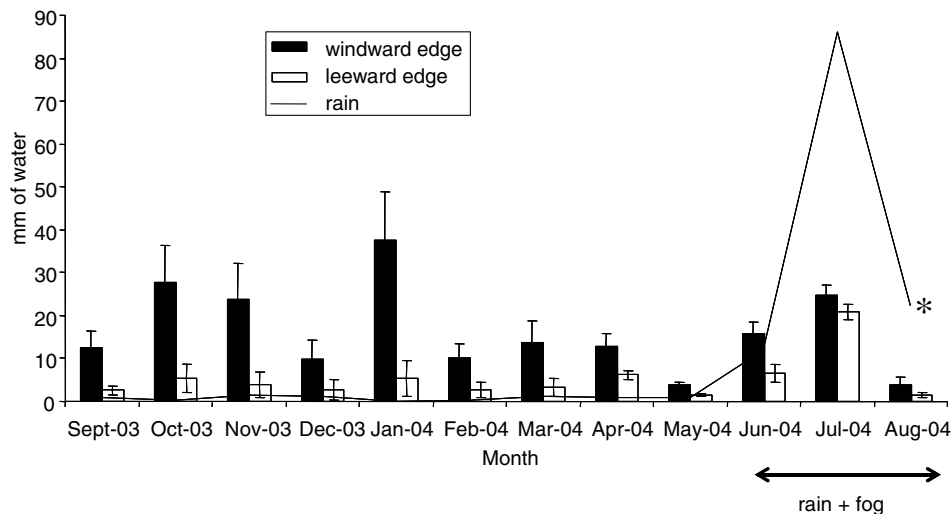


Figure 2. Accumulated millimeters of water captured by fog collectors over a 12-month period in windward and leeward edges of five forest patches. Mean volume of water captured (mm, precipitation equivalents) per month \pm 1 SE and precipitation records (rain + fog) from Quebrada Las Vacas meteorological station, Fray Jorge (J. R. Gutiérrez and F. López unpublished) are shown. Asterisk indicate average precipitation from the closest three meteorological stations (Romeral, Doca, and Lilen), La Serena (approximately 70 km from Fray Jorge National Park) (http://www.ceaza.cl/Ceaza-Met/index_html). Note that between June and August 2003 water captured by fog collectors contained a larger proportion of rainwater.

using position, month, and position \times month interaction as explanatory variables, nested by forest patch and by month.

Tree regeneration (seedling and sapling densities), adult density, and total basal area of canopy trees were compared among WE, LE, and FI transects using a nested ANOVA; nesting factors were forest patch and transect position. Differences in minimum age of Olivillo trees among transects were assessed by one-way ANOVA. The volume of CWD in WE, LE, and FI of transects was compared by a nested ANOVA with patch and transect position as nesting factors. All analyses were performed on log-transformed data, to correct for nonnormality, using S-PLUS 2000 (Math Soft Inc.).

RESULTS

Fog-Water Inputs

Water captured by the PFC throughout the year (2003–2004) was greatest at the edge of forest patches facing the prevailing westerly winds (Figure 2). Substantially less fog-water was collected at the opposite, LE, of the patches than in the WE, indicating a strong fog-shadow effect. The WE enhancement (that is, WE:LE fog-capture ratio) ranged from 6.3 (in November) to 1.2 (in July, the month with greatest rainfall). Seasonally, January 2004, which is the austral midsummer, had the highest fog-water capture (19% of the total amount

of water collected throughout the year of study). The lowest fog-water capture values (2%) were obtained in early winter, May 2004 ($F_{(11,44)} = 15.3$, $P < 0.001$). Overall, fog-water captured at the WE was on average 3.1-fold greater than that captured at the LE ($F_{(1,48)} = 30.32$, $P < 0.001$) (Figure 3a). The interaction between month and edge effect was statistically significant ($F_{(11,48)} = 2.41$, $P = 0.01$), indicating that the contrast in fog-water inputs between patch edges increases in months with greater fog influx. Water collected in the LE was relatively less variable throughout the year, whereas WE water interception showed greater seasonal variability. Months with the greatest fog capture corresponded with dry-summer months of low rainfall, and this pattern was translated into a more or less continuous water capture by PFC throughout the year (Figure 2).

Relationships between Water Interception and Tree Regeneration

The distribution of tree seedlings within patches was strongly related to the direction of fog inputs. Tree seedling density was significantly higher in the WE and FI than in the LE of all patches (Figure 3b). Windward edge and FI transects had similar tree seedling densities (mean, 9.2 ± 4.7 individuals/m² and 10.9 ± 5.2 individuals/m², respectively); these values were three-fold higher than seedling densities in the LE (mean, 3.2 ± 1.48 individuals/m²;

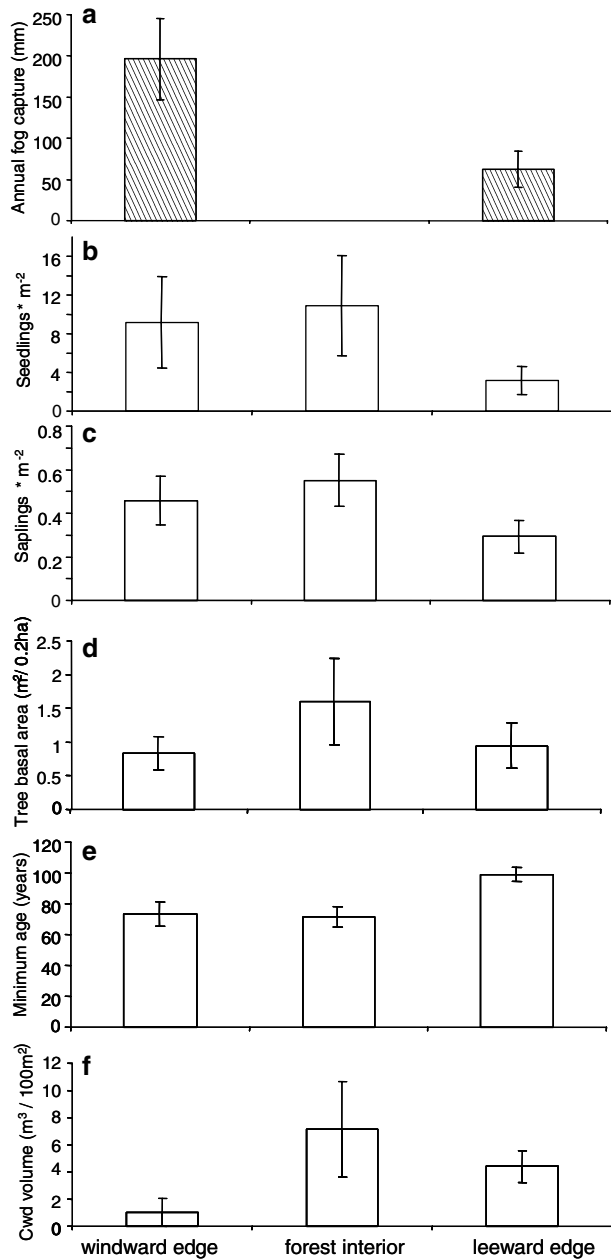


Figure 3. Forest structural attributes associated with fog-input direction. **a** Total water captured by fog collectors (mean mm \pm 1 SE); **b** total seedling density per m² (mean \pm 1 SE); **c** Total sapling density per m² (mean \pm 1 SE); **d** Live tree basal area (m²) per transect (mean basal area \pm 1 SE); **e** Minimum tree ages for Olivillo (mean \pm 1 SE), $n = 77$; **f** Volume of coarse woody debris (m³ per 100 m²) in different transects inside the forest (mean \pm 1 SE).

$F_{(2,10)} = 5.3, P = 0.03$). Seedling distribution for most individual species tended to be concentrated toward the WE or FI (Figure 4a); but because of the low seedling densities and high spatial variation of seedlings between forest patches, the effect was not

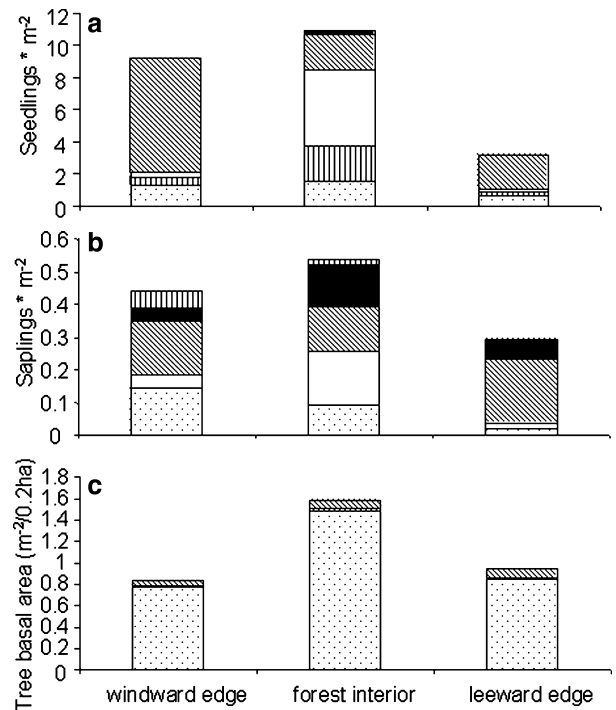


Figure 4. Distribution of tree abundance and regeneration in relation to fog-input direction for five different tree species. **a** Seedling density (individuals per m²); **b** Sapling density (individuals per m²); **c** Adult tree basal area (m²/0.2 ha). Dotted bar indicates *Aextoxicon punctatum*, Vertical bar indicates *Azara microphylla*, empty bar indicates *Drymis winteri*, hatched bar indicates *Myrceugenia correifolia*, Filled bar indicates *Rraphithamnus spinosus*.

significant for seedlings of *A. punctatum* ($F_{(2,10)} = 1.94, P = 0.19$), *A. microphylla* ($F_{(2,10)} = 0.86, P = 0.45$), *D. winteri* ($F_{(2,10)} = 2.5, P = 0.13$), and *M. correifolia* ($F_{(2,10)} = 1.33, P = 0.3$). Seedlings of *R. spinosus* were rare and present only in the FI (Figure 4a).

Sapling densities within patches showed the same trend as seedling in relation to fog-input direction (Figure 3c), although differences between edges and interior were not statistically significant ($F_{(2,10)} = 1.34, P = 0.3$). As a main effect, fog-input direction was not significantly different for sapling distributions of individual species ($P > 0.05$); but after collapsing factor levels (WE + FI versus. LE), we found that *A. punctatum* saplings were concentrated in the WE and FI transects ($F_{(1,5)} = 11.4, P = 0.02$), whereas *A. microphylla* saplings were concentrated at the WE ($F_{(1,5)} = 8.2, P = 0.03$) (Figure 4b).

Adult Tree Densities and Basal Areas in Relation to Fog Input

For *A. punctatum* ($F_{(2,10)} = 0.75, P = 0.5$), *A. microphylla* ($F_{(2,10)} = 1.12, P = 0.36$), *D. winteri*

($F_{(2,10)} = 1.32$, $P = 0.31$) and *R. spinosus* ($F_{(2,10)} = 0.88$, $P = 0.44$), adult tree densities did not vary significantly with transect position relative to fog-input direction (Figure 4c). However, adult trees of *M. correifolia* were more frequent in patch edges than in the FI ($F_{(2,10)} = 5.52$, $P = 0.02$), (Figure 4c).

Although the total basal area of adult trees tended to be higher in the FI, it did not differ statistically among transect positions with respect to fog direction ($F_{(2,10)} = 0.75$, $P = 0.49$) (Figure 3d). Adult tree biomass was strongly dominated by *A. punctatum* in all transects and forest patches (that is, more than 88%, of the basal area).

Tree Ages

Minimum ages of Olivillo trees in each patch differed significantly among transects ($F_{(2,74)} = 4.4$, $P = 0.02$). Older trees were concentrated toward the LE of forest patches (WE + FI versus. LE: $F_{(1,75)} = 8.92$, $P = 0.003$; Figure 3e).

Coarse Woody Debris

Although the overall trend across all three positions with respect to fog input was unrelated to CWD volume ($F_{(2,10)} = 2.82$, $P = 0.11$), when combined FI + LE was compared to WE there was a significant difference in CWD volume (one-way ANOVA, $F_{(1,11)} = 6.1$, $P = 0.03$). This indicated that cover and volume of snags and logs was greater in the FI and LE of the forest patches than in the edge facing the fog (WE) (Figure 3f).

DISCUSSION

Relationship between Fog and Forest Structure

Our results indicate strong correlations between the areas of a forest patch that first receive fog-water inputs (WE) and measures of forest structure and regeneration. All forest patches had new tree establishment concentrated in the WE (or fog-receiving edge), where oceanic fog inputs are three-times higher than in the opposite edges, thus providing a suitable microhabitat for seedling and sapling growth. In contrast, tree mortality was largely concentrated in the patch center and particularly in the edges opposite to fog-input direction (LE), where the oldest trees in the patch are found. Our data suggest that reduced fog-water interception in the LE of patches may explain why higher mortality and reduced tree regeneration occur there. In the central portion of patches, un-

der closed canopy, mortality seems to be due predominantly to canopy shading on small trees. Further, as indicated by the minimum-age estimates, patches located on the summit plateau of the coastal range may be growing in the direction of the incoming fog, and hence "moving" across the landscape as they track the fog inputs growing towards the front and dying at the back of the patch. The pattern of greater fog incidence during dry-summer months is of critical importance for the persistence of the forest because evergreen, broad-leaved trees could be subjected to extreme water stress during months of zero rain precipitation. Consequently, fog becomes the only hydric source sustaining this forest during dry annual periods (October to April). This pattern of greater fog inputs in summer seems to be consistent among years (P. Vidiella unpublished data). Cereceda and others (1997) have documented that fog is more abundant during the austral summer in northern Chile because the altitude of the Pacific inversion layer is higher in summer than winter, consequently promoting the movement of fog toward the continent, where it encounters the Coastal mountain range during summer (where forest patches are present), whereas the inversion layer stays close to the sea surface in winter.

Edge Effect and Fog Shadows

Studies of forests influenced by cloud-water inputs in other regions of the world have also documented enhanced water interception at windward forest edges compared to FI (Beier and Gunderson 1989; and others Erisman and others 1997; Weathers and others 1992, 1995, 2000, 2001). The pronounced fog-shadow effect documented for the patches in Fray Jorge is very similar to previous findings showing that most water gets intercepted in the first few meters of the WE of the patch, declining steeply toward the opposite edge.

Estimates of Fog-Water Input

Our estimates of fog-water inputs, using artificial PFC, when converted to millimeters of rainfall, suggest that trees may be receiving an additional input of approximately 200 mm of water annually. It is important to note that the PFC used here do not mimic actual forest structure and are unlikely to accurately estimate total fog-water deposition to these forests (even though their use enabled us to standardize collection surfaces and to compare fluxes between WE and LE locations). The projected surface area per unit ground area of the PFC is likely to be substantially less than that of the

actual vegetation, in which case our estimate of approximately 200 mm of extra water input per year probably underestimates fog capture by these forests. If this estimated value of fog interception is used, the combined water inputs (147 mm rain + 200 mm fog) result in a total water input commensurate with that usually required for tree growth and survival (that is, 300–400 mm).

Fog Inputs and Ecosystem Persistence

Fog subsidies to total water inputs, especially in the WE of patches, may be sufficient to explain, at least in part, the unexpected persistence of this rainforest in the Chilean semiarid region, where the regional climate would otherwise prevent it. Conditions of strong aridity, as found today, began in this region during the late Tertiary, becoming more intense during the interglacial periods of the Pleistocene, whereas glacial periods were more humid and presumably favored the transitory expansion of Olivillo forests to lower elevations (Villagrán and others 2004). Olivillo forests would have persisted through the long, dry interglacial using fog-water subsidies, as they do now during shorter intervals of severe drought associated with the negative phases of ENSO (Jaksic 2001; Montecinos and Aceituno 2003). As little as 2.2 mm of rainfall in 1 year have been recorded during La Niña episodes in the Fray Jorge area (Meserve and others 2003), underscoring the key role of incoming fog for forest persistence.

Because ecosystem development at this latitude is constrained primarily by the limited supply of rainwater to plants, current tree regeneration should be constrained to zones with greater fog-water capture and retention. This pattern of regeneration contrasts with that found in the southern range of Olivillo forests, where tree regeneration is generally limited by light availability (Veblen and others 1981; Armesto and Fuentes 1988). Examples of such switches from light limitation to water limitation of tree growth have been documented for *Nothofagus pumilio* at its northeastern distribution limit in the Andes (Heinemann and others 2000) and for *Austrocedrus chilensis* in the forest–steppe boundary in northern Patagonia (Kitzberger and others 2000). In the Patagonian semiarid ecotone, *Austrocedrus* can germinate only under nurse shrubs, which provide moist microsites (Kitzberger and others 2000). These examples illustrate how rainforest trees that evolved in light-limited environments may have been forced to adapt in recent times to increasing aridity (Villagrán and Varela 1990; Maldonado and Villagrán

2002). Under the present extreme aridity of FJNP, these new constraints should be reflected in tree growth patterns and in the present forest patch structure.

Tree Species Distribution within Patches

Differences in distribution within patches among tree species presumably reflect their differential tolerances to canopy shading and moisture availability. The most hygrophilous species, *D. winteri*, which has an extended southern distribution in wet temperate forests reaching 55°S (Villagrán and Armesto 1980), tends to be aggregated in the interior of larger forest patches and did not occur in small patches. On the other hand, adult individuals of *Aextoxicon punctatum* and *Azara microphylla* occur only in the edge directly receiving fog influx, as well as in the FI. Finally, *M. correifolia* was generally associated with patch edges, regardless of fog input direction. *Myrceugenia correifolia* may be the most drought resistant tree species in this rainforest assemblage, as is common in patch edges, and it is also distributed mainly in the mediterranean-climate region of central Chile and not in southern rainforests at higher latitudes (Villagrán and others 2004). These observations are also consistent with leaf carbon–nitrogen (C:N) ratios reported for tree species in Fray Jorge forests by Pérez (1996). Carbon–nitrogen ratios are used as an index of sclerophylly and tolerance to drought because a higher ratio represents greater leaf mass, higher crude fiber contents, greater leaf hardness, and lower rates of water loss (Loveless, 1961). Higher indices of sclerophylly have been reported for *A. punctatum* and *M. correifolia*, whereas *D. winteri* and *R. spinosus* had less sclerophyllous leaves (Pérez 1996).

Our results show that the persistence of the mosaic of forest patches in FJNP depends on the continuity of fog presence in the region. In general, our data lend support to the idea that Fray Jorge forest structure and regeneration patterns reflect the present climate and are not declining, as previously suspected by other authors (Gajardo and others 1984; Gajardo and Grez 1990), because tree regeneration is occurring in all patches, there are trees across age classes to 200 years old, and we found no indication of an overall decline in tree density within forest patches.

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