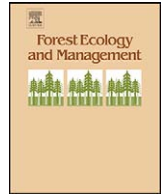




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Environmental variables influencing regeneration of *Nothofagus pumilio* in a system with combined aggregated and dispersed retention

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ABSTRACT

The current silvicultural prescriptions for *Nothofagus* are designed to stimulate natural regeneration by opening the canopy. One of these methods is variable retention, which can include either or both aggregated and dispersed retention. Different degrees of retention may modify microclimatic variables differently and consequently offer dissimilar microenvironmental conditions for regeneration. Retained canopy influences both biotic and abiotic factors. The objective was to evaluate *Nothofagus pumilio* regeneration along edge-related gradients within aggregated retention, and in the different microenvironments within the harvested areas. The remnant canopy cover after harvesting greatly influenced regeneration mainly by decreasing radiation transmittance and soil moisture availability. Aspect (direction to the azimuth) and distance from edge of aggregates influenced regeneration density, height and growth. In dispersed retention, microenvironments generated by different types of understory plant cover, debris, and proximity of remnant trees also influenced regeneration. High levels of understory cover (up 50%) and medium levels of harvesting debris cover (25–50%) had a positive impact, while close proximity to remnant trees had a negative impact on regeneration. These findings can be used to improve silvicultural and harvesting prescriptions to ensure successful establishment of regeneration and maximize potential growth.

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1. Introduction

Silvicultural prescriptions for *Nothofagus pumilio* forests are based on canopy opening to stimulate natural regeneration (Martínez Pastur et al., 2007). The two most commonly applied systems are traditional type shelterwoods and, more recently, variable retention. Variable retention has been designed to conserve the original biodiversity and at least part of the original heterogeneity of the natural old-growth forests (Franklin et al., 1997; Lencinas et al., 2009). As applied in Tierra del Fuego, this system leaves 25–30% of the harvested area as aggregated retention and 15–20% basal area as dispersed retention (Martínez Pastur et al., 2009).

Retained aggregates create different microenvironments in the harvested areas by modifying the microclimate, natural biogeochemical cycles and physical processes. The magnitude of this change depends on the distance from the aggregates, the under-

story cover type, harvesting debris and the proximity of retained trees (Chen et al., 1993, 1995; Heithecker and Halpern, 2007). These microenvironments present differing conditions for regeneration, where light and soil moisture availability are the most important factors determining establishment, growth and eco-physiological performance (Heinemann et al., 2000; Heinemann and Kitzberger, 2006; Lencinas et al., 2007; Martínez Pastur et al., 2007; Peri et al., 2009). Light availability is mainly modified by canopy opening and remnant overstorey spatial distribution (Caldentey et al., 2009; Promis et al., 2010). However, understory cover, microtopography and edaphic properties (e.g., organic matter) may be more important than overstorey structure for modifying soil moisture availability (Heithecker and Halpern, 2007).

Therefore, in this study the objective was to evaluate the influence on *Nothofagus pumilio* regeneration of edge effects, understory cover, harvesting debris and proximity of retained trees in a variable retention system during the first 6 years after harvesting. Tested hypotheses were (i) aggregated retention modifies microclimate and influences regeneration according to aspect (direction to the azimuth) and distance from the edge, and (ii) microenvironments in variable retention determine regeneration growth, whereas understory cover and harvesting debris have a positive effect, and retained trees have a negative effect.

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2. Methods

2.1. Study sites and microclimate characterization

Data were obtained from three study sites located in pure old-growth *Nothofagus pumilio* forests in advanced development phase (up to 200 years) in Tierra del Fuego Island (Argentina). These forests were harvested to a variable retention prescription (Martínez Pastur and Lencinas, 2005; Martínez Pastur et al., 2009), where aggregated (one 30 m radius aggregate retained per hectare) and dispersed retention (10–15 m² ha⁻¹ basal area of the most dominant trees distributed between the aggregates) were left as remnant overstorey after harvesting. The study sites were located in San Justo Ranch (54°06'S, 68°37'W) harvested six years before the study commenced, Los Cerros Ranch (54°18'S, 67°49'W) harvested four years, and Río Irigoyen Forest Reserve (54°36'S, 66°37'W) harvested two years.

The climate is characterized by short, cool summers and long, snowy winters. Only three months per year are free of mean daily air temperatures under 0°C, and the growing season is approximately five months. Rainfall, including snowfall, reaches up to 600 mm yr⁻¹. Annual average wind speed outside forests is 8 km h⁻¹, reaching up to 100 km h⁻¹ during storms (Barrera et al., 2000; Martínez Pastur et al., 2009). To characterize the microclimate within the variable retention harvesting areas, three data loggers (model H8, HOBO, USA with soil temperature probe and shield radiation) were used at San Justo Ranch to measure air temperature at 1 m height and soil temperatures at 30 cm soil depth, over one year in: (i) the interior of retained aggregates (–10 m from the edge) (AR), (ii) the dispersed retention within the influence of the aggregate (10 m from the edge) (DRI), and (iii) the dispersed retention beyond the influence of the aggregate (20 m from the edge) (DR). To analyze rainfall percentage according to the wind direction during storms at each site, three weather stations (Weather Wizard III and accessories, Davis Instruments Corp., USA) were located in an open area inside the forests. The stations were located at San Justo Ranch (years 2002–2004), Los Cerros Ranch (years 2005–2009) and María Cristina Ranch (years 1996–2000) (54°29'S, 66°10'W). Because there is no available climate data for Río Irigoyen Forest Reserve, the nearest available climatic information, located 38 km west at María Cristina Ranch, was used to characterize the site.

2.2. Regeneration measurements

At each study site, four aggregates in the harvested areas were selected. In each aggregate, regeneration plots of 1 m² (500 × 20 cm) were recorded according to aspect (N, E, S and W) and distance (–10, 10 and 20 m) from the aggregate edges (3 sites × 12 treatments × 4 replicates). Sampling was designed to analyze the influence of AR, DRI and DR areas and aspect on regeneration (Fig. 1). For this work, seedlings have been defined as 1-year-old plants, and saplings as plants >1-year-old and less than 1.3 m height. In each plot, density, height and age of each plant were measured. Age was determined in the field from annual growth scars in the stems (Cuevas, 2002; Gea et al., 2004), while height was measured from the base to the top of the longest extended shoot. Mean annual height growth of each plant was estimated using individual total height and age. Natural browsing of *Lama guanicoe* occurs in the study area (Pulido et al., 2000). The studied stands were of middle to high site quality according to Martínez Pastur et al. (1997), and before harvesting had a total over-bark volume of between 700 and 900 m³ ha⁻¹ and dominant total heights of between 20.5 and 27.5 m (Martínez Pastur et al., 2009).

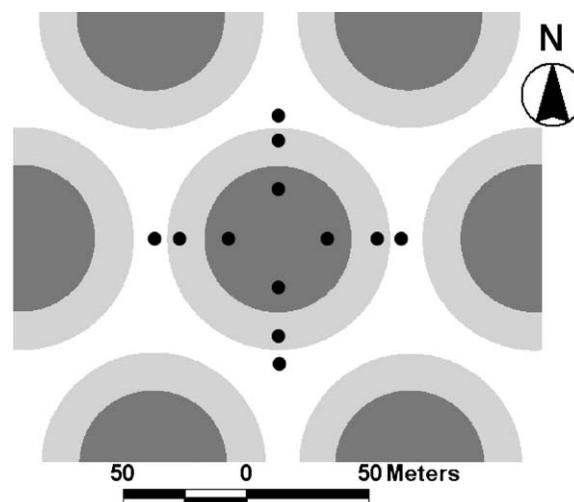


Fig. 1. Distribution of plots according to the aspect and distance from the aggregated retention edge in *Nothofagus pumilio* forests. Sampling area was divided in aggregated retention (circular aggregates of 30 m radius) (dark grey), dispersed retention within the influence of aggregated retention (<15 m to the edge) (light grey), and dispersed retention beyond the influence of aggregated retention (>15 m to the edge) (white).

2.3. Microenvironment stand characterization

Each regeneration sampling plot was divided into five sectors along the major axis (100 × 20 cm each), and the dominant understorey cover type (U) (recorded as normal for <50% plant cover and >50% soil or litter without vegetation cover, as dicotyledonous for >50% plant cover with dicotyledonous dominance, and as monocotyledonous for >50% plant cover with monocotyledonous dominance), harvesting debris (D) (absence, <25%, 25–50%, and >50% cover) and proximity of retained trees (proximity of trees <2 m, and trees at longer distances) were recorded. Basal area (BA) (m² ha⁻¹) using a Criterion RD-1000 (Laser Technology, USA) with a variable K between 3 and 7, and volumetric soil water content (VSW) (%) using a MP406 moisture probe (ICT, Australia) were also measured in each plot during middle summer (January).

To characterize canopy structure and solar radiation transmission, hemispherical photographs of forest canopy were taken at 1 m above ground level with an 8 mm fish eye lens (Sigma, Japan) mounted on a 35 mm digital camera (Nikon, Japan) with a tripod leveling head to ensure horizontal lens position. Each photograph was orientated with the upper edge towards the north. Photographs were taken with no direct sunshine early in the morning or on cloudless days (Roxburgh and Kelly, 1995). Gap Light Analyzer software v.2.0 (Robison and McCarthy, 1999; Frazer et al., 2001) was used to define: crown cover (CC) as a percentage of open sky relative to forest canopy; effective leaf area index (LAI) integrated over the zenith angles 0–60° (Stenburg et al., 1994); global radiation (GR) at understorey level as the amount of direct and diffuse radiation transmitted through the canopy along the growing season (November–March), and percentage of global radiation (PGR) as the ratio of GR and the amount of direct and diffuse radiation incident on a horizontal surface located above forest canopy. The following user-supplied input variables were used: (a) specific projection distortion provided by lens manufacturing company; (b) a sky-region grid compound by 20 azimuth and 4 zenith regions; (c) a constant value of 1367 W m² for total radiant flux of sun outside the Earth's atmosphere (Hardya et al., 2004) and clear-sky transmission coefficient (factor that describes the regional clarity of the atmosphere with respect to instantaneous transmission of direct radiation) of 0.6; (d) cloudiness index (site-specific measured cloudiness), spectral fraction (ratio of solar energy that falls within limited range

of the electromagnetic spectrum to the total shortwave radiation contributed by all wavelengths) and beam fraction (ratio of direct to global spectral radiation incident on horizontal surface) were obtained from radiation data (years 2004–2005) provided by Universidad de Magallanes (Santana, 2006; Santana et al., 2006) and VAG-Ushuaia (Global Atmospheric Watch Station).

2.4. Statistical analysis

Three-way ANOVAs were carried out using aspect (N, E, S and W), distance from aggregate edge (–10, 10 and 20 m) and studied sites (ST) as the main factors to analyze BA, VSW, CC, LAI, GR, PGR, as well as the regeneration dynamic variables: regeneration density (R) (thousand ha^{-1}) (seedlings + saplings), sapling density (S) (thousand ha^{-1}), regeneration mean age (RA) (years), sapling mean age (SA) (years), regeneration mean height (RH) (cm), sapling mean height (SH) (cm), regeneration mean height growth (RG) (cm year^{-1}) and sapling mean height growth (SG) (cm year^{-1}). Complementary, two-way ANOVAs were done using ST, U , D and RT as main factors to analyze R , S , RA, SA, RH, SH, RG and SG. A post hoc Tukey's test, corrected for unequal N , was used for all mean comparisons ($P < 0.05$). Finally, an analysis of the regeneration dynamic variables in the harvested sectors with dispersed retention of saplings was performed using a canonical correspondence analysis (CCA) (Ter Braak and Šmilauer, 2002) to estimate components of variance contributed by edge-related gradients in aggregated retention and relationships of microenvironments in dispersed retention. The significance of direct gradient CCA ordination was tested using Monte Carlo techniques. In the ordination, plots were classified according their mean $H > 1$ ($< 2.5 \text{ cm year}^{-1}$, $2.6\text{--}5.0 \text{ cm year}^{-1}$, and $> 5.1 \text{ cm year}^{-1}$). Selected explicatory variables for microenvironment stand characterization were BA, VSW, CC, LAI, GR, U , D , RT and ST.

3. Results

3.1. Microclimate and stand variation

Soil temperatures in spring and summer were higher in DR (20 m from the edge) than DRI (10 m from the edge) than AR (–10 m from the edge); maximum values were 11.9°C , 11.2°C and 10.5°C , respectively. During autumn and winter, soil temperature decreased to a minimum in the harvested areas (DR and DRI with -0.3°C) compared to AR (0.7°C), which did not show temperatures below zero (Fig. 2). Maximum and minimum air temperatures had similar trends to those described for soil temperatures, but with less variation among treatments. Extreme values were observed in DR with maximum air temperature varying between 2.7°C in July and 19.9°C in February, while DRI presented values between 2.5°C in July and 19.5°C in February, and AR presented values between 2.1°C in July and 19.2°C in February. The lowest minimum air temperature values were in DR between -6.6°C in July and 5.9°C in February, while DRI presented values between -6.2°C in July and 5.9°C in February, and AR presented values between -5.6°C in July and 6.2°C in February (Fig. 2).

Dominant wind direction during storms was not homogeneous, but varied among sites. At San Justo Ranch, the most western study site, most of the rainfall occurred with E to SE wind storms (37% of the rainfall) followed by WSW to WNW aspects (26%). At Los Cerros Ranch, rainfall pattern changed, because wind storms came from N to NE (30%) and from ENE to SE (30%). At María Cristina Ranch, the most eastern study site, 52% of the rainfall corresponded to wind storms coming from NNW to NE (Fig. 3).

While aspect did not show significant differences for microclimate and stand variables, significant differences were found for ST

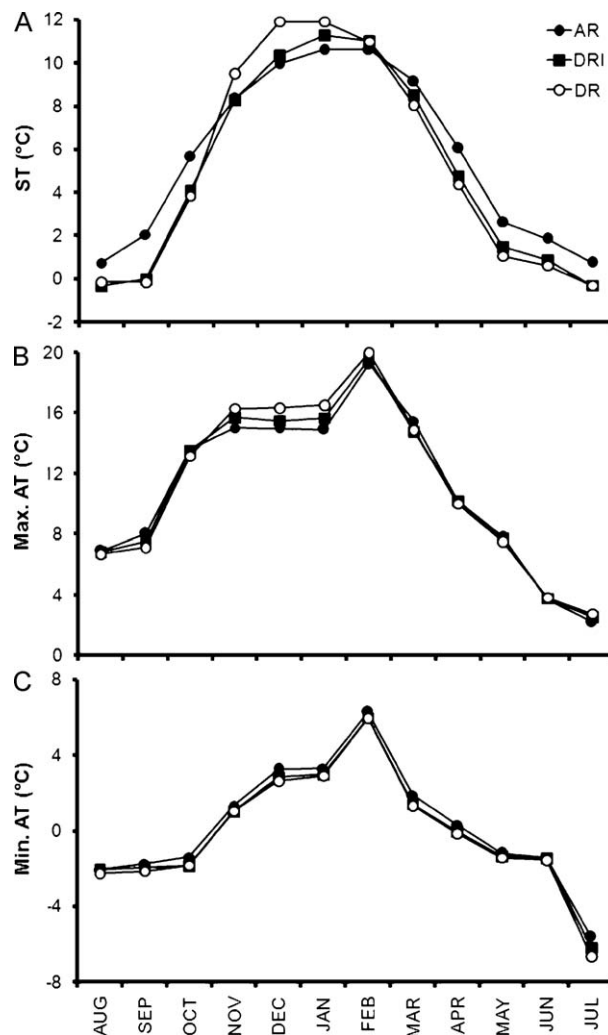


Fig. 2. Soil temperature (ST) (A), maximum air temperature (Max. AT) (B) and minimum air temperature (Min. AT) (C) in aggregated retention (AR), dispersed retention within the influence of aggregated retention (DRI), and dispersed retention beyond the influence of aggregated retention (DR) over one year in *Nothofagus pumilio* forests.

and distance from the edge of aggregates (Table 1). BA and VSW decreased with years after harvesting at each ST. The other variables (CC, LAI, GR and PGR) varied at different sites, which can be related to windthrow and growth of remnant tree canopies after harvesting. While VSW, GR and PGR changed proportionally to the distance from the edges of aggregates, BA, CC and LAI were inversely proportional (Table 1).

3.2. Edge-related gradients of aggregated retention influence over regeneration dynamics

Significant differences were found for regeneration variables when ST, aspect and distance from edge were analyzed (Table 2). When aspect was considered, R was higher in the north and west sectors of the aggregates ($405\text{--}425 \text{ thousand ha}^{-1}$) and lower in south ($201 \text{ thousand ha}^{-1}$), RH–SH were higher in north sectors ($17\text{--}19 \text{ cm}$) and lower in east (11 cm), as well as RG–SG (5.1 cm year^{-1} and 3.7 cm year^{-1} in north and east, respectively) (Table 2). All the studied variables varied significantly when ST was considered. Age (RA and SA) and height (RH and SH) were related to the years after harvesting, while density (R and S) and growth (RG and SG) were related to the sites (Table 2). When distance from edge was considered, density (R and S)

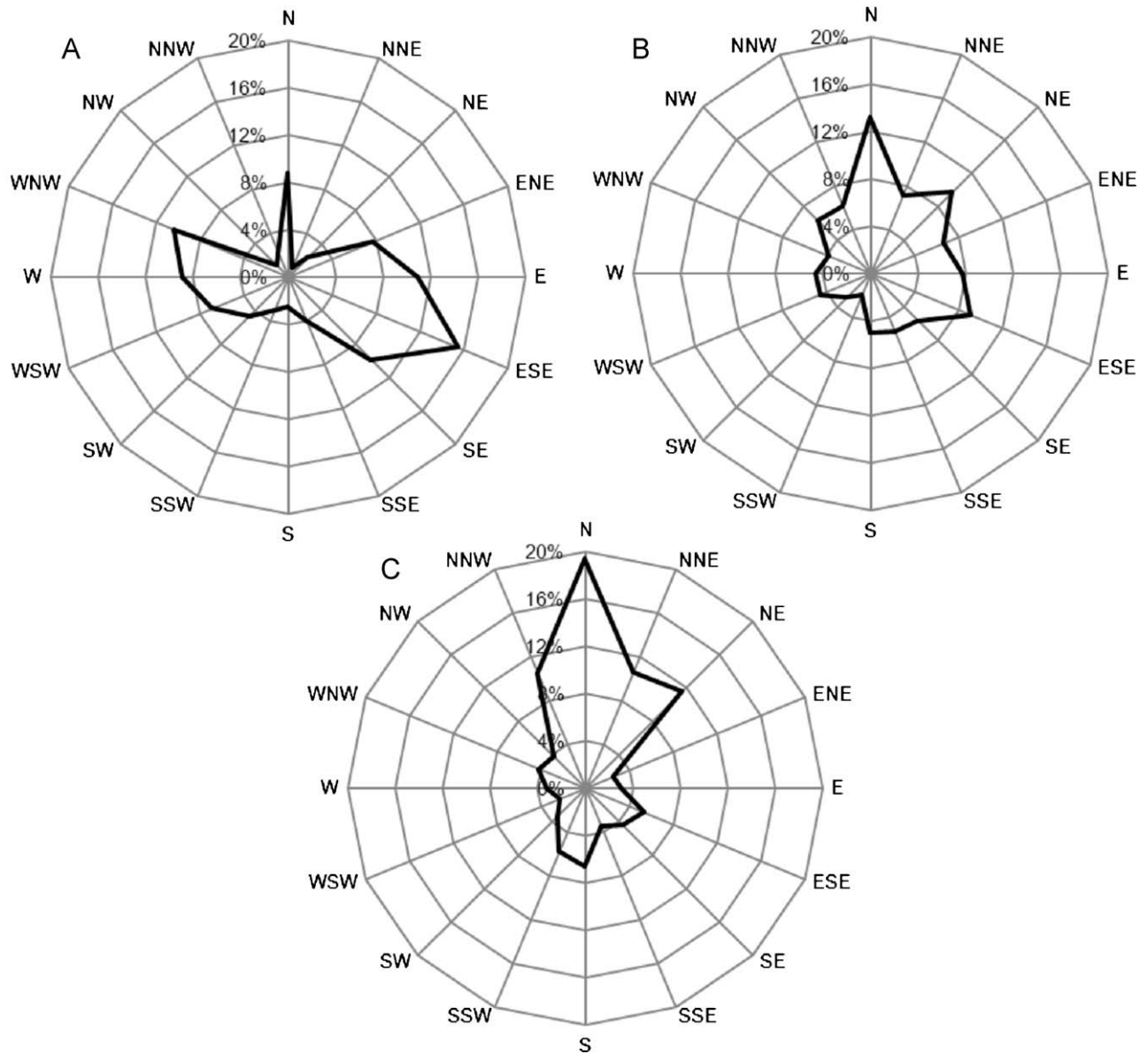


Fig. 3. Rainfall percentage according to the wind direction during storms in three sites of Tierra del Fuego: San Justo Ranch (A), Los Cerros Ranch (B) and María Cristina Ranch (C).

Table 1

Three-way ANOVAs and means for studied sites (ST) (RI = Río Irigoyen Ranch, LC = Los Cerros Ranch and SJ = San Justo Ranch), aspect (N, E, S and W) and distance from edge (m) in the aggregated retention as main factors, for basal area (BA) ($m^2 ha^{-1}$), volumetric soil water content (VSW) (%), crown cover (CC) (%), effective leaf area index (LAI), global radiation (GR) ($W m^2$) and percentage of global radiation (PGR) (%) at understory level transmitted through the canopy in *Nothofagus pumilio* forests.

Factor		BA	VSW	CC	LAI	GR	PGR
A: ST	RI	39.45 b	29.92 b	61.74 b	1.13 b	17.78 a	45.86 a
	LC	27.18 a	36.47 b	57.85 a	0.93 a	20.14 b	51.94 b
	SJ	28.54 a	20.59 a	60.88 ab	1.11 ab	18.90 ab	48.72 ab
	<i>F</i> (<i>p</i>)	16.30 (<0.001)	14.22 (<0.001)	3.28 (0.041)	3.96 (0.022)	5.00 (0.008)	4.98 (0.008)
B: Aspect	N	29.91	33.76	60.24	1.13	19.58	50.60
	E	35.58	25.90	59.96	1.11	18.52	47.81
	S	31.86	30.48	61.96	1.04	18.01	46.22
	W	29.69	25.83	58.46	0.96	19.65	50.73
	<i>F</i> (<i>p</i>)	2.02 (0.115)	2.48 (0.064)	1.21 (0.308)	1.42 (0.240)	1.73 (0.165)	1.96 (0.125)
C: Distance	-10	61.72 c	19.34 a	77.00 c	1.96 c	9.62 a	24.88 a
	10	18.81 b	33.69 b	55.18 b	0.73 b	21.75 b	56.05 b
	20	13.75 a	33.95 b	48.29 a	0.49 a	25.45 c	65.59 c
	<i>F</i> (<i>p</i>)	247.59 (<0.001)	15.61 (<0.001)	175.90 (<0.001)	198.49 (<0.001)	244.64 (<0.001)	243.45 (<0.001)
A × B × C interactions	<i>F</i> (<i>p</i>)	1.61 (0.099)	0.83 (0.618)	1.07 (0.389)	1.54 (0.120)	1.11 (0.362)	1.09 (0.379)

F = Fisher test; (*p*) = probability. Letters indicate differences using Tukey test (*P* = 0.05).

Table 2
Three-way ANOVAs and means for studied sites (ST) (RI = Río Irigoyen Ranch, LC = Los Cerros Ranch and SJ = San Justo Ranch), aspect (N, E, S and W) and distance from edge (m) in the aggregated retention as main factors for regeneration density (R) (thousand ha⁻¹), sapling density (S) (thousand ha⁻¹), regeneration mean age (RA) (years), sapling mean age (SA) (years), regeneration mean height (RH) (cm), sapling mean height (SH) (cm), regeneration mean height growth (RG) (cm year⁻¹) and sapling mean height growth (SG) (cm year⁻¹) in *Nothofagus pumilio* forests.

Factor		R	S	RA	SA	RH	SH	RG	SG
A: ST	RI	483.75 b	260.00 ab	2.26 a	2.83 a	8.14 a	9.77 a	3.46 a	3.35 a
	LC	131.25 a	117.71 a	2.69 b	2.89 a	15.96 b	17.30 b	5.38 b	5.58 b
	SJ	416.45 b	404.58 b	3.37 c	3.42 b	16.08 b	16.18 b	3.75 a	3.73 a
	F(p)	14.40 (<0.001)	11.11 (<0.001)	21.73 (<0.001)	7.64 (<0.001)	9.44 (<0.001)	7.54 (<0.001)	10.59 (<0.001)	13.53 (<0.001)
B: Aspect	N	405.55 ab	292.22	2.87	3.21	17.44 b	18.91 b	5.06 b	5.10 b
	E	343.05 ab	253.33	2.62	2.85	10.78 a	11.39 a	3.72 a	3.69 a
	S	201.38 a	165.56	2.91	3.16	13.91 ab	15.05 ab	4.17 ab	4.26 ab
	W	425.27 b	331.94	2.70	2.98	11.45 ab	12.33 a	3.84 ab	3.85 ab
	F(p)	3.16 (0.027)	2.05 (0.111)	0.97 (0.410)	1.56 (0.203)	3.15 (0.028)	3.96 (0.010)	2.83 (0.042)	2.95 (0.036)
C: Distance	-10	638.33 b	454.16 b	2.37 a	2.72 a	5.56 a	6.28 a	2.39 a	2.25 a
	10	217.91 a	171.45 a	2.78 b	3.06 ab	14.51 b	15.92 b	4.51 b	4.55 b
	20	175.21 a	156.66 a	3.17 b	3.37 b	20.12 c	21.05 c	5.70 c	5.77 c
	F(p)	26.93 (<0.001)	15.18 (<0.001)	10.83 (<0.001)	7.72 (<0.001)	24.47 (<0.001)	25.74 (<0.001)	28.63 (<0.001)	31.61 (<0.001)
A × B × C interactions	F(p)	1.26 (0.254)	1.18 (0.303)	1.08 (0.387)	0.90 (0.546)	0.85 (0.603)	0.79 (0.660)	0.47 (0.929)	0.46 (0.935)

F = Fisher test; (p) = probability. Letters indicate differences using Tukey test (P = 0.05).

decreased from inside towards outside sectors, while the other variables increased (Table 2). Inside AR (-10 m plots, which corresponded to 24% of the harvested stand area) (Fig. 1) the higher R-S values were observed (638–454 thousand ha⁻¹) with lower age, height and growth (2.4–2.7 years, 5.6–6.3 cm and 2.4–2.2 cm year⁻¹ for regeneration and saplings, respectively). In DRI (10 m plots, which corresponded to 38% of the harvested stand area), intermediate values were observed for density, age, height and growth (218–171 thousand ha⁻¹ plants with 2.8–3.0 years, 15–16 cm height and 4.5–4.6 cm year⁻¹ growth). Finally, in DR (20 m plots, which corresponded to 38% of the harvested stand area), lower density values were observed (175–157 thousand ha⁻¹ for R and S, respectively) with higher age, height and growth (3.2–3.4 years, 20–21 cm and 5.7–5.8 cm year⁻¹ for R and S, respectively). Significant interactions were not detected for the whole analysis.

3.3. Influence of microenvironment and stand variables on regeneration dynamic

Variable retention harvested areas present different microenvironments, which can influence the regeneration (average ± standard deviation): (i) 23.7% ± 2.3% of the area was occupied by aggregated retention, (ii) 17.4% ± 6.0% of the area corresponded to skidder paths, (iii) 3.0% ± 1.3% of area was under the influence of remnant trees in the dispersed retention, (iv) 40.4% ± 8.4% of the area was covered by harvesting debris (21.3% large debris, 40.6% medium debris, 38.1% small branches), and (v) 15.4% ± 1.6% corresponded to other conditions (37.7% normal, 59.0% covered by dicotyledonous and 3.3% by monocotyledonous plants). Most of these microenvironment types influenced regeneration (Table 3). As described previously, ST affected most of the regeneration variables. Understory cover type influenced seedling and sapling growth (RG and SG), being greater under monocotyledonous (7.0–7.3 cm year⁻¹) than under dicotyledonous (5.4–5.6 cm year⁻¹) than in a normal cover (4.6–4.7 cm year⁻¹). Harvesting debris negatively influenced regeneration establishment (252–259 thousand ha⁻¹ in low levels compared to 82–141 thousand ha⁻¹ in medium-high levels), but positively influenced height (14–15 cm in low levels vs. 18–22 cm in medium-high levels of debris). Height growth also increased under harvesting debris shelter, being higher under medium (25–50%) cover (6.2 cm year⁻¹). Proximity of retained trees also

influenced the regeneration and sapling mean height (7.4–8.1 cm) and their growth (2.3 cm year⁻¹) compared with areas without remnant trees (17.4–18.8 cm and 5.2–5.4 cm year⁻¹, respectively).

Mean height growth of saplings can be explained through CCA analysis performed with four regeneration variables (S, SA, SH, and SG) in the harvested sectors with dispersed retention (Fig. 4). In this analysis, nine environmental explicatory variables were used, and their individual significance presented the following order: ST > D > RT > U > LAI > VSW > CC > GR > BA. The final model of the analysis had an F-ratio = 10.78 with P = 0.006. The eigenvalue of the axis 1 was 0.052, while axis 2 presented a value < 0.001. The plots-environment correlations reached to 0.529 for axis 1 and 0.310 for

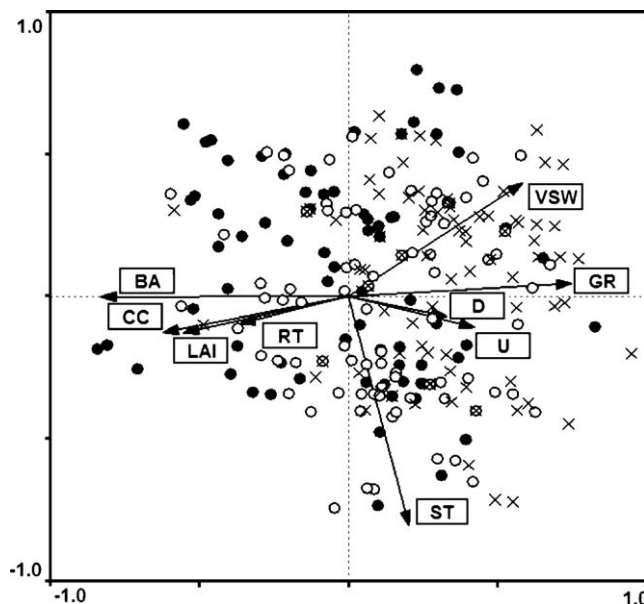


Fig. 4. CCA analysis for regeneration dynamic variables of saplings (>1-year-old plants) in the harvested sectors with dispersed retention in *Nothofagus pumilio* forests. Plots were classified according their mean height growth (black dots = < 2.5 cm year⁻¹, white dots = 2.6–5.0 cm year⁻¹, cross = > 5.1 cm year⁻¹). Environmental explanatory variables were studied sites (ST) (years after harvesting), basal area (BA) (m² ha⁻¹), volumetric soil water content (VSW) (%), crown cover (CC) (%), effective leaf area index (LAI), global radiation (GR) (W m²), influence of the understory cover type (U) (%), harvesting debris (D) (%) and proximity of retained trees (RT).

Table 3

Two-way ANOVAs and means for studied sites (ST) (RI=Río Irigoyen Ranch, LC=Los Cerros Ranch and SJ=San Justo Ranch) and influence of the understory cover type (NORMAL=<50% plant cover, DICO=>50% dicotyledonous dominance cover, MONO=>50% monocotyledonous dominance cover), harvesting debris (0=absence, 1=<25%, 2=25–50%, 3=>50% cover) and proximity of retained trees (YES=trees within <2 m, NO=longer distances to the nearest trees) in the harvested sectors with dispersed retention for regeneration density (*R*) (thousand ha⁻¹), sapling density (*S*) (thousand ha⁻¹), regeneration mean age (*RA*) (years), sapling mean age (*SA*) (years), regeneration mean height (*RH*) (cm), sapling mean height (*SH*) (cm), regeneration mean height growth (*RG*) (cm year⁻¹) and sapling mean height growth (*SG*) (cm year⁻¹) in *Nothofagus pumilio* forests.

Factor		<i>R</i>	<i>S</i>	<i>RA</i>	<i>SA</i>	<i>RH</i>	<i>SH</i>	<i>RG</i>	<i>SG</i>
Influence of understory cover									
A: ST	RI	228.98 b	170.22 b	2.47 a	2.78 a	17.36	18.5	6.60 b	6.58 b
	LC	78.04 a	68.67 a	2.56 a	2.93 a	18.25	21.45	6.13 b	6.71 b
	SJ	209.28 b	204.13 b	3.70 b	3.77 b	20.03	20.36	4.37 a	4.40 a
	<i>F</i> (<i>p</i>)	5.26 (0.005)	7.30 (<0.001)	16.72 (<0.001)	9.76 (<0.001)	0.35 (0.703)	0.21 (0.814)	6.92 (0.001)	8.34 (<0.001)
B: Cover	NORMAL	222.76	189.43	2.79	3.02	15.26	16.39	4.64 a	4.75 a
	DICO	171.32	138.11	2.91	3.16	17.85	19.40	5.47 a	5.62 a
	MONO	122.22	115.47	3.04	3.30	22.52	24.51	7.00 b	7.32 b
	<i>F</i> (<i>p</i>)	1.81 (0.165)	2.09 (0.124)	0.41 (0.662)	0.59 (0.556)	1.83 (0.162)	2.12 (0.121)	4.44 (0.012)	4.47 (0.012)
A × B interactions	<i>F</i> (<i>p</i>)	1.33 (0.259)	1.77 (0.133)	0.55 (0.700)	0.42 (0.797)	2.40 (0.049)	2.21 (0.068)	5.12 (0.001)	4.75 (0.001)
Influence of debris									
A: ST	RI	270.08 b	196.37 b	2.44 a	2.78 a	10.51 a	11.52 a	4.07 a	3.98 a
	LC	68.53 a	62.48 a	2.63 a	2.86 a	20.20 b	22.40 b	6.85 b	7.27 b
	SJ	212.19 b	207.54 b	3.58 b	3.65 b	21.35 b	21.95 b	4.79 a	4.88 a
	<i>F</i> (<i>p</i>)	14.17 (<0.001)	12.23 (<0.001)	19.84 (<0.001)	13.01 (<0.001)	11.72 (<0.001)	11.35 (<0.001)	12.74 (<0.001)	15.45 (<0.001)
B: Debris	0	258.77 b	204.62 b	2.85	3.13	14.75 a	15.88 a	4.62 a	4.66 a
	1	252.20 b	211.28 b	2.80	3.10	14.15 a	16.27 ab	4.52 a	4.80 a
	2	141.22 a	131.10 ab	3.21	3.13	22.15 b	22.55 b	6.22 b	6.22 b
	3	82.21 a	74.85 a	2.67	2.85	18.36 ab	19.79 ab	5.59 ab	5.83 ab
	<i>F</i> (<i>p</i>)	7.27 (<0.001)	5.50 (0.001)	1.70 (0.166)	0.91 (0.438)	4.01 (0.008)	2.78 (0.041)	4.20 (0.006)	3.34 (0.019)
A × B interactions	<i>F</i> (<i>p</i>)	2.83 (0.010)	2.60 (0.017)	2.31 (0.033)	2.33 (0.032)	1.77 (0.105)	2.16 (0.046)	1.11 (0.358)	1.23 (0.292)
Influence of closeness of remnant trees									
A: ST	RI	322.79 b	231.71 b	2.40 a	2.84 a	8.82 a	10.14	3.55	3.47
	LC	41.15 a	37.34 a	2.80 a	2.93 a	12.40 ab	13.70	3.68	4.44
	SJ	277.90 b	266.24 b	3.51 b	3.66 b	16.04 b	16.61	4.18	3.72
	<i>F</i> (<i>p</i>)	10.22 (<0.001)	8.44 (<0.001)	10.76 (<0.001)	6.19 (0.002)	3.10 (0.046)	2.27 (0.105)	0.14 (0.867)	0.33 (0.718)
B: Trees	YES	376.31	201.34	2.91	3.16	7.39 a	8.12 a	2.36 a	2.35 a
	NO	269.26	155.53	2.90	3.13	17.46 b	18.84 b	5.24 b	5.39 b
	<i>F</i> (<i>p</i>)	1.17 (0.280)	1.11 (0.292)	0.01 (0.963)	0.01 (0.935)	5.78 (0.016)	6.27 (0.013)	10.65 (0.001)	10.95 (0.001)
A × B interactions	<i>F</i> (<i>p</i>)	1.01 (0.363)	1.02 (0.359)	0.94 (0.392)	0.58 (0.562)	1.41 (0.247)	1.39 (0.250)	1.56 (0.211)	1.74 (0.178)

F=Fisher test; (*p*)=probability. Letters indicate differences using Tukey test (*P*=0.05).

axis 2. Ordination graphic showed that BA > CC > LAI > RT influenced negatively in SG, while GR > VSW > U > D positively affected SG, that was mainly correlated with axis 1. Finally, ST allowed separate plots along the axis 2 according to the magnitude of each variable.

4. Discussion

4.1. Microclimate and stand structure variation

The microclimatic conditions in *Nothofagus pumilio* stands following different degrees of retention was variable, as has been shown for other forests (Chen et al., 1999; Heithecker and Halpern, 2006, 2007). In this study, more extreme values of soil and air temperature were found in DR compared to AR. Harvested areas surrounding aggregates (DRI) resulted in intermediate temperatures, while soil moisture and radiation significantly increase to similar DR values compared to AR. However, the supposition that edge microclimate presents intermediate values between harvested areas and interior forests contrasts with the results of Chen et al. (1993), who found this for wind velocity and solar radiation, and not for temperature and moisture. The microclimate variations of our study were related to remnant forest structure, where aggregates offer additional shelter to DRI compared to DR. Harvesting modified microclimate through the alteration of

the overstorey canopy, increasing temperature, radiation and soil moisture (Richter and Frangi, 1992; Caldentey et al., 2005, 2009; Promis et al., 2010). Temperature, humidity, soil moisture, short-wave radiation, and wind velocity change from harvested forests to edges and adjacent interior forest environments (Chen et al., 1993; Heithecker and Halpern, 2006, 2007). Contrary to our findings, Chen et al. (1993) observed greater soil moisture in a control Douglas-fir forest than in a harvested one or in the edge, while Heithecker and Halpern (2007) determine that soil moisture exhibited no spatial trends among aggregates, harvest areas, and controls. Temperature, radiation and soil moisture are the most critical factors (Lieffers et al., 1999) that affect growth and survival of seedlings in these austral forests (Heinemann et al., 2000; Martínez Pastur et al., 2007). Also, these factors influence decomposition and natural cycles (Barrera et al., 2000; Caldentey et al., 2001), as well as biodiversity conservation (e.g., forest soil under undisturbed overstorey canopies does not freeze during the year allowing several insect and plant species to survive the winter season) (Spagarino et al., 2001; Martínez Pastur et al., 2002).

Wind direction during storms is not homogeneous in Tierra del Fuego, where rainfall spatial distribution is determined by the interception of remnant trees in the variable retention. Aggregates differentially influence the amount of rainfall interception according to aspect, generating different VSW levels. Undisturbed

canopies of *Nothofagus pumilio* forests intercept 25% of rainfall during summer season (20% during whole year) (Frangi and Richter, 1994), while 30 m² ha⁻¹ basal area of remnant overstorey decreases the interception to 16% (Caldentey et al., 2005). The amount of rainfall interception determines the quantity of water that reaches the forest floor, and consequently the soil moisture available for seedlings and saplings (Martínez Pastur et al., 2007). The rainfall pattern determined in this study changes among the studied sites, due to the influence of northeastern Atlantic oceanic storms rather than the sub-polar climate. However, usually Tierra del Fuego climate is defined as belonging to southern anti-boreal zone (Tuhkanen, 1992), where storms come from south.

In shelterwood and dispersed retention cuts, stand conditions were homogenized due to systematical canopy removal (Martínez Pastur et al., 2000). By contrast, variable retention with aggregates and dispersed retention maintains some of the natural heterogeneity of the original forests (Martínez Pastur et al., 2009). For example, the relationship of aggregate edge to the azimuth introduces another spatial source of spatial light heterogeneity (Chen et al., 1999; Heithecker and Halpern, 2007). Although significant differences were not detected in spatial light distribution, trends do exist. In the high latitudes of Southern Hemisphere, such as in Tierra del Fuego, the sun path is closer to the horizon, so the influence of aggregates on spatial light patterning would be higher, producing larger shadows than in lower latitudes. Southerly aspects present more shaded areas compared to northerly ones, with less potential evapotranspiration. Similarly, aggregates receive more precipitation in the direction of dominant winds during storms due to rainfall interception. More soil moisture would be expected in windward aggregate aspects during storms, while leeward aspects were drier. This influence on microclimate was also described for microenvironments and aspects inside the gaps (Heinemann et al., 2000; Heinemann and Kitzberger, 2006).

4.2. Effect of edge-related gradients of aggregated retention on regeneration dynamics

Regeneration inside the aggregates presents the same characteristics of the seedling bank of *Nothofagus pumilio* primary unmanaged forests in Tierra del Fuego (Martínez Pastur et al., 1999; Cuevas, 2002; Gea et al., 2004), e.g. high density, young age, short height and slow annual growth. These forests do not present a seed bank in forest soil (Cuevas, 2002), and continuous recruitment and mortality in the seedling bank annually occurs. In contrast, regeneration density is lower in harvested dispersed retention areas (DR) mainly due to harvesting damage or self-thinning (Martínez Pastur et al., 1999; Rosenfeld et al., 2006), increasing average age, height and annual growth due to the survival of the established plants. Areas close to aggregates (DRI) provide additional shelter from unfavorable conditions (drought, excessive radiation or strong winds) for regeneration, e.g. while age and regeneration densities are similar to DR, height and annual growth show intermediate values between DR and AR.

Regeneration survival and growth depends on the species eco-physiological characteristics. *Nothofagus pumilio* is considered as mid-shade tolerant in early development stages (Gutiérrez, 1994) as it reaches maximum photosynthetic efficiency at relatively low light levels (26% of total incident irradiance) (Martínez Pastur et al., 2007). Other forest species also require shelter to increase their recruitment, survival rate and growth, for example *Fagus sylvatica* increases these variables across a gradient from clear-cuts to dense shelterwood cuts in Sweden (Agestam et al., 2003). Mortality of western white pine in North America is higher in the harvested areas between aggregates, probably due to their relatively harsh conditions. This effect was stronger at 40% than at 15% retention, suggesting that aspect and other factors must have contributed to

these mortality patterns (Maguire et al., 2006). For these reasons, regeneration response in aggregate and dispersed retention may change according to species characteristics.

The relationship of aggregate edge to the azimuth influenced regeneration. Plant density was higher on the northern and western sides of aggregates, probably due to (i) dominant wind direction during seeding (March–April) (Martínez Pastur et al., 2008), (ii) higher soil moisture due to rainfall interception by the aggregates, and (iii) greater light availability. On the other hand, height and growth were higher on the northern and southern sides of aggregates. The benefit of north aspects (higher soil moisture and light availability) is added to the south aspects which had less potential evapotranspiration for shaded areas. Recruitment, survival and growth have been related to water stress (Heinemann et al., 2000; Heinemann and Kitzberger, 2006), or waterlogging affecting their biomass compartmentalization (Lencinas et al., 2007) and photosynthetic performance (Sun et al., 1995; Martínez Pastur et al., 2007; Peri et al., 2009).

4.3. Effect of microenvironment in harvested stand on regeneration dynamic

High spatial variation in harvested forests, including aggregates, suggests that heterogeneity in understory cover, microtopography, and edaphic properties (e.g., organic matter) is likely to be more important than overstorey structure in determining soil moisture availability (Heithecker and Halpern, 2007). These microenvironments in harvested stands offer dissimilar conditions for regeneration dynamics, due to the influence of biotic and abiotic factors. Small amounts of debris provide additional shelter for regeneration establishment and allowed them to obtain better growth, but with lower seedling recruitment. In contrast, larger amounts of debris negatively influence the regeneration due to shading of light, but large woody debris can act as nurse logs (Heinemann and Kitzberger, 2006). Similarly, remnant trees in harvested areas offer shelter to the regeneration inside their crown influence. However, there is a negative influence close to the trees (<2 m), e.g. in RH–SH and RG–SG. This could be explained by a decrease in soil moisture availability due to water uptake by the remnant trees (mean VSW to the growth season was 11.6% close to trees compared to 29.3% further away from the influence of the trees, data not shown). Rainfall interception increases with canopy closure, and consequently decreases available soil moisture for seedlings (Wardle, 1970, 1974; Martínez Pastur et al., 2007). Finally, understory plant species may act as facilitators or competitors, increasing or reducing impacts of stressful environments (Heinemann and Kitzberger, 2006). In our study, high understory covers (>50%) positively influence RG–SG, being more favorable under grasses (e.g., *Festuca gracillima* Hooker f.) than herbs (e.g., *Osmorhiza depauperata* Phil.).

4.4. Implications for silvicultural management

The current silvicultural prescriptions for *Nothofagus* forests are based mainly on opening the canopy to stimulate natural regeneration by modifying soil moisture and light availability at the understory level (Martínez Pastur et al., 2000, 2009). The best retention strategy for establishment and growth of an understory cohort, therefore, varies by species and stage of seedling development. If retention of overstorey trees proves successful for sustaining biodiversity, a balance must be struck among functional integrity of the forest ecosystem, timber yield, and ensuring adequate survival and growth of regeneration (Messier et al., 1999; Maguire et al., 2006). During the last ten years, a variable retention method was proposed for *N. pumilio* forests (Martínez Pastur and Lencinas, 2005; Martínez Pastur et al., 2009). This method conserves some of the original

heterogeneity of the original forests. The presence of aggregated retention benefits biodiversity conservation (e.g., Lencinas et al., 2009), but also influences regeneration. Effects of aspect on microclimatic variation suggest that patch shape and orientation can be used to advantage, for example in temperate regions to reduce the area susceptible to elevated light and temperature. Although a circular shape minimizes the ratio edge/area, the strong directionality of solar radiation and associated increases in temperature, mainly in high latitudes, suggest that an ellipsoid would minimize the area subjected to edge effects, and thus the area in which adverse biological effects are most likely to occur (Heithecker and Halpern, 2007). For these, future application of silvicultural systems must take into account the changes in both factors (light and soil moisture) due to the presence of remnant overstorey and their distribution patterns to maximize the potential growth of natural regeneration.

Regeneration density values measured in this work should be enough to fully regenerate the harvested stands (e.g., the recommended rate is more than 40 thousand ha⁻¹) (Martínez Pastur et al., 1999; Rosenfeld et al., 2006). However, the survival rate and growth can be improved by modifying stand conditions after harvesting through: (i) varying the spatial distribution of remnant trees in the variable retention according to the site conditions (e.g., by taking into account the dominant winds during storms and seeding months), (ii) ensuring the homogeneous debris distribution at the furthest distances from the aggregates, where regeneration needs additional shelter, and (iii) by retaining the most suitable overstorey crown cover to allow a convenient understory development to facilitate regeneration growth.

5. Conclusions

Remnant canopy cover after harvesting greatly influences regeneration, mainly through lower radiation transmittance and soil moisture availability. The variable retention system, which combines dispersed and aggregated retention, influences on microclimate and consequently on regeneration. Aggregates produce edge effects proportionally to their distance (e.g., seedlings had the highest density in the dispersed retention within the influence of the aggregate) and aspect (e.g., seedlings had the highest density and grew best on the north aspect), while dispersed retention gives protection but also negatively influence over regeneration according to their closeness. In harvested areas, understory cover and debris, also influence regeneration giving additional shelter and improving sapling growth. These findings can be used to improve silvicultural and harvesting prescriptions to ensure regeneration establishment and maximization of their potential growth.

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