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Seed production and recruitment in primary and harvested *Nothofagus pumilio* forests: Influence of regional climate and years after cuttings

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Abstract

Aim of study: Harvesting proposals (e.g. variable retention) for *Nothofagus pumilio* forests are based on canopy opening, to increase recruitment and enhance seedling growth, by modifying light and soil moisture. Seed production and seedling recruitment will define the success of harvesting, where remnant forest structure are the main influence factors, as well as biotic and abiotic factors. The objective was to analyse seed production, seedling recruitment and recruitment efficiency in primary and harvested forests through variable retention along the first 10 years after harvesting, as well as the influence of regional climate.

Area of study: The study were conducted in a pure *Nothofagus pumilio* forest located in central Tierra del Fuego (54°18' S, 67°49' W), where harvested stands with variable retention and unmanaged forests were sampled in long-term permanent plots.

Material and methods: Data of forest regeneration plots were used (n = 72) (2007 a 2014), and forest structure and seed production (2006 a 2013) were also measured. Regional climate was characterised for these years from satellite images (Sea Surface Temperature) and climate re-analysis models (rainfall and temperature of land surface).

Main results: Harvesting modified forest structure; however, aggregated retention maintained some characteristics of the primary unmanaged forests. These changes influenced seed production and recruitment. Seed production and recruitment were related to crown cover and the amount of seed production; however, recruitment efficiency was not affected by harvesting. The studied variables significantly changed along the years after harvesting. Seed production and recruitment were also related to regional climate factors, where it was possible to explain their variations through temperature (e.g. summer temperature) and rainfall (e.g. winter rainfall) for the different retention types in harvested forests and the primary forests.

Research highlights: Variable retention harvesting generated different micro-conditions that influence seed production and recruitment. These variables were related to canopy cover. However, recruitment efficiency was not affected by harvesting. Seed production and recruitment (primary forests and harvested stands) were related to regional climate factors and their variations can be explained from variables related to temperature and rainfall.

Key words: regeneration; forest management; crown cover; regional climate; modelling; Tierra del Fuego.

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Introduction

Nothofagus pumilio (Poepping & Endl.) Krasser forests regenerate mainly from natural seeds, and eventually from agamic propagation in some special environmental conditions, e.g. tree-line in upper mountains (González *et al.*, 2006; Ivancich *et al.*, 2012). There is

a lack of seed bank in these forests because seeds quickly lose their viability (Cuevas & Arroyo, 1999). However, a seedling bank can be found and it survives for many years waiting for the canopy opening (Cuevas, 2000, 2002). Natural succession in timber forests is based on gap dynamics (Rebertus & Veblen, 1993), where pre- and post-recruitment regeneration increas-

es abundantly when a disturbance occurs (Gutiérrez, 1994). Harvesting proposal is based on this canopy opening to stimulate seedling recruitment and natural regeneration by modifying light availability and soil moisture (Martínez Pastur *et al.*, 2009, 2011a). The remaining canopy has multiple functions such as mitigating micro-climatic conditions inside the harvested stands (Chen *et al.*, 1993, 1995), providing seeds in the harvested areas (Cellini, 2010), or as legacies for conservation (Lindenmayer *et al.*, 2012).

The first years after harvesting are crucial for the future trees recruitment that will recover the forest structure of the harvested stands (Martínez Pastur *et al.*, 2011a,b), where the balance between light availability and soil moisture together with ice damage in sprouts, will determine survival and growth of the recruited seedlings. Besides, seed production is not homogeneous among years (Cellini, 2010) neither at landscape nor at stand scale (Martínez Pastur *et al.*, 2013). Seeding cycles were described for many forest species, including *Nothofagus* genera (Monks & Kelly, 2006) where variation among years is especially high (Kelly, 1994; Kelly & Sork, 2002). There are different hypothesis about the reasons behind these seeding cycles, including physiological and climatological driving factors (Isagi *et al.*, 1997; Liebhold *et al.*, 2004; Bahamonde *et al.*, 2011).

Light and soil moisture levels in the harvested stands, as well as the degree of protection of the remaining canopy, are determined by the employed silvicultural management plan (Martínez Pastur *et al.*, 2011a,b). Some harvesting systems homogenize the stands (e.g. shelterwood cuts) while others try to maintain some of the heterogeneity of the natural forests (e.g. variable retention) (Lindenmayer *et al.*, 2012; Martínez Pastur *et al.*, 2013). The diversity of micro-environments generated with variable retention, combining aggregates and dispersed retention, greatly influences recruitment, survival and seedling growth. It is possible to observe differential synergies (positive or negative) according to micro-sites, e.g. regeneration performance is significantly different when it is compared within-aggregates and in the harvested areas close and far away from the influence of the aggregates (Hörnberg *et al.*, 1997; Kupfershmid & Bugmann, 2005; Blood & Titus, 2010; Vodde *et al.*, 2010; Martínez Pastur *et al.*, 2011b, 2012).

The objective of this work was to analyze seed production (SEE), seedling recruitment (REC) and recruitment efficiency (EF) (ratio between seedling recruitment and seed production) in unmanaged primary *Nothofagus pumilio* forests and harvested stands using variable retention, after a decade from cuttings in relation to regional climate variability (rainfall, and tem-

peratures of land and sea surface). Through this study we want to answer the following questions regarding seed production, seedling recruitment and recruitment efficiency: (i) is there a differential impact over these variables in the harvest stands with variable retention compared to primary unmanaged forests?; (ii) is there any change for the different retention types in the harvested stands along the years after the cuttings?; (iii) do seedling recruitment and recruitment efficiency change according to seed production?; and (iv) is the regional climate a driving factor?.

Materials and methods

Regeneration data taking and forest structure

Data was taken in a pure *Nothofagus pumilio* forest harvested through variable retention (Martínez Pastur *et al.*, 2009) located in the Isla Grande of Tierra del Fuego (Argentina). This harvesting method retains a percentage of the original forest structure, leaving aggregates (a circular patch of 30 m radius per ha) and dispersed dominant trees (10-15 m².ha⁻¹ of basal area) evenly distributed between the aggregates. The forest of medium site quality (dominant height of 22-24 m) is located in Estancia Los Cerros (54°18' S, 67°49' W), and before harvesting it presented a range of 700-900 m³.ha⁻¹ of timber volume and 70-80 m².ha⁻¹ of basal area (Martínez Pastur *et al.*, 2009). This forest belongs to a long-term permanent plot of a network in Patagonia Sur (PEBANPA, Parcelas de Ecología y Biodiversidad de Ambientes Naturales en Patagonia Austral, INTA-CONICET, Argentina) (Martínez Pastur *et al.*, 2010). Regeneration permanent plots (500 x 20 cm) established in primary unmanaged forests (PF) (n = 18) and harvested stands 10 years ago with variable retention (n = 54) were used. In the harvested forests, the plots were located covering 3 different conditions according to the retention levels (see Martínez Pastur *et al.*, 2011b): (i) within-aggregate retention (AR) (n = 18), in the dispersed retention under the influence of the aggregated retention (<20 m from the aggregates edges) (DRI) (n = 18), and in the dispersed retention far away the influence of the aggregates (DR) (n = 18).

Seedling recruitment was recorded during summer from 2007 to 2014. Moreover, litter traps were placed close to each plot (50 x 30 cm) to collect seeds during May of each year from 2006 to 2013. Dominant height (DH) was taken in each plot by Impulse Laser Range-finder (Laser Technology, US), basal area (BA) using a Criterion RD-1000 (Laser Technology, US) with a

K-coefficient between 1 and 6. Total over bark volume (TOBV) was estimated using equations proposed by Martínez Pastur (2006) with stand basal area and site quality as independent variables. Hemispherical photos were taken to estimate canopy cover (CC) and relative leaf area index (RLAI) integrated over the zenith considering an angle between 0° and 60° (Stenburg *et al.*, 1994). The photos were taken at a height of 1 m above the ground with 8-mm fisheye lens (Sigma, Japan) mounted on a 35-mm digital camera (Nikon, Japan), and were analyzed with Gap Light Analyzer v.2.0 software (Robison & McCarthy, 1999; Frazer *et al.*, 2001). The program was supplemented with a distortion projection provided by the lens manufacturer, and a division of the sky composed of 20 azimuths and zenith 4 regions was used.

Regional climate data

There is a lack of local climate information for the study area, for this we use data from regional climate using satellite images. Different data sources were used to characterize this regional climate between years 2006 and 2013: (i) For the Argentine sector of Isla Grande de Tierra del Fuego, data from the re-analysis NCEP (National Center for Environmental Prediction) of NOAA (National Oceanic and Atmospheric Administration) were used: average monthly air temperature data near earth surface (0.995 sigma level) with a spatial resolution of 2.5°; and average monthly precipitation (precipitable water) was obtained from the same source and resolution, since this data source provides more consistent and continuous information for areas with little climate information (Kalnay *et al.*, 1996). (ii) For the sea surrounding Isla Grande de Tierra del Fuego (48°55' to 59°24' S and 54°52' to 76°16' W), data of Sea Surface Temperature (SST) were obtained from NASA Ocean Color. This service provides information on monthly composite SST re-sampled to 4-km from version 3 of SST product of nighttime images of the original MODIS (1-km resolution and 3 scenes daily). Climate data were averaged by month (PP = precipitation, T = temperature, S = temperature of sea surface), and were analyzed considering minimum (MIN), maximum (MAX) or annual mean values (A) (April to March of the following year); and according to summer (SUM = October to March of the following year) or winter (WIN = April to September) seasons. For seed recruitment and efficiency data (SEE, REC, EF), values were correlated with the climate of summer of the corresponding season either with the previous winter or with the sum of both in the case of annual data.

Statistical analysis

Three analysis of variance (ANOVA) were performed: (i) for different forest types (PF, AR, DRI, DR) considering forest structure and canopy variables (DH, BA, TOBV, CC and RLAI); (ii) for different forest types (PF, AR, DRI, DR) considering seed production and recruitment variables (SEE, REC, EF); and (iii) years after harvest (3 to 10 years) considering seed production and recruitment variables (SEE, REC, EF). Beside this, multiple ANOVA considering forest types (PF, AR, DRI, DR) and relative seed production according to magnitude of seed rain (1 = low, 2 = medium, 3 = high) was performed to analyze data of seed production and recruitment variables (SEE, REC, EF). Differences between factor means were compared using Tukey test ($p < 0.05$).

A canonical correspondence analysis (CCA) was performed (terBraak & Šmilauer, 2002) with seed production, recruitment (SEE, REC, EF), and regional climate data. The objective of this analysis was to: (i) estimate how much the regional climate values influenced the variance of seed production and recruitment data, and (ii) identify those regional climate variables with the highest influence for each group. The significance of the CCA analysis was quantified by Monte Carlo test, where 499 permutations were performed for each model. The most significant variables in each multivariate analysis were used to adjust linear regressions without origin coefficient for the different seed production and recruitment variables (SEE, REC, EF) and forest types (PF, AR, DRI, DR). To evaluate the adjustment of each equation, the significance of the coefficients, the r^2 -adj., the standard error of the estimation (SEE) and the mean absolute error (MAE) were considered.

Results

Forest structure and canopy cover

Significant differences were detected in all the studied variables (Table 1). Dominant height was slightly higher in the harvested forests (aprox. 24.0 m) compared to primary unmanaged forests (22.2 m). Basal area and volume was higher in PF, intermediate in AR, and significantly lower in harvested areas (DRI and DR). Canopy cover also presented significant differences among all the treatments, with a gradient from PF and from within the aggregates to the farthest areas in the dispersed retention. Finally, relative leaf area index did not present any differences between PF and

Table 1. Forest structure (DH = dominant height, BA = basal area, TOBV = total over bark volume, CC = crown cover, RLAI = relative leaf area index) of the unmanaged primary forests (PF) and harvested stands with variable retention (AR = aggregated retention, DRI = dispersed retention under the aggregate influence, DR = dispersed retention without aggregate influence).

	DH (m)	BA (m ² .ha ⁻¹)	TOBV (m ³ .ha ⁻¹)	CC (%)	RLAI
PF	22.2 a	75.4 c	857.1 c	88.2 d	2.51 b
AR	23.9 b	45.2 b	597.6 b	80.3 c	2.30 b
DRI	24.0 b	12.3 a	194.0 a	51.2 b	0.62 a
DR	24.0 b	8.5 a	138.8 a	44.5 a	0.39 a
<i>F(p)</i>	3.70(0.016)	107.23(<0.001)	79.31(<0.001)	231.85(<0.001)	275.60(<0.001)

F = Fisher test; (p) = probability. Different letters showed differences at $p < 0.05$ with Tukey test.

AR, which were significantly higher than in the harvested areas (DRI and DR).

Seed production and recruitment

When all the studied years were analyzed together, significant differences were found in the seed production and seedling recruitment for the different forest types (Table 2). The higher values were recorded in PF, followed for the AR and the harvested areas (DRI and DR). However, in the seedling recruitment the AR and dispersed retention areas did not present significant differences. Finally, no significant differences were found for the recruitment efficiency among forest types. However, when considering the inter-annual variations for all the harvested treatments (AR, DRI and DR) significant differences were detected among years for the three studied variables (Table 3). These differences did not follow an uniform pattern, due to years of high (e.g. year 4 after cutting) or low (e.g. year 9 after cutting) seed production were recorded.

When recruitment variables were considered (REC and EF) to compare relative production of seeds in the different forest types (in PF: 1 = 0-3, 2 = 3-12, and

3 = > 12 mill.ha⁻¹.year⁻¹; in AR: 1 = 0-3, 2 = 3-10, and 3 = > 10 mill.ha⁻¹.year⁻¹; in DRI: 1 = 0.0-0.8, 2 = 0.8-2.5, and 3 = > 2.5 mill.ha⁻¹.year⁻¹; in DR: 1 = 0.0-0.5, 2 = 0.5-1.5, and 3 = > 1.5 mill.ha⁻¹.year⁻¹) significant differences were detected for both variables in PF, increasing REC and EF as SEE increased. No differences were found in the harvested forests, except for the REC in DR, where it significantly increased with SEE (Table 4).

Relationships among regional climate, seed production and recruitment

The canonical correspondence analysis (CCA) for seed production (Table 5 and Fig. 1) showed a total inertia of 0.21 (eigenvalue of axis 1 = 0.09 and of axis 2 = 0.02) explaining with both axes 53% of the variation in seed production by forest types, and 98% of the variation in seed production by regional climate. The Monte Carlo test presented a $F(p) = 2.38(0.048)$. The climatic variables with higher significance were the average precipitation during winter (PP-A-WIN), the

Table 2. ANOVAs for the seed production (SEE), recruitment of seedlings (REC) and recruitment efficiency (EF) of the unmanaged primary forests (PF) and harvested stands with variable retention (AR = aggregated retention, DRI = dispersed retention under the aggregate influence, DR = dispersed retention without aggregate influence).

	SEE (mill.ha ⁻¹ .year ⁻¹)	REC (n.m ² .year ⁻¹)	EF (%)
PF	10.98 c	28.0 b	1.46
AR	8.29 b	13.2 a	1.68
DRI	2.62 a	3.3 a	1.66
DR	1.47 a	1.9 a	1.39
<i>F(p)</i>	41.06(<0.001)	14.89(<0.001)	0.08(0.971)

F = Fisher test; (p) = probability. Different letters showed differences at $p < 0.05$ with Tukey test.

Table 3. ANOVAs for the seed production (SEE), recruitment of seedlings (REC) and recruitment efficiency (EF) of harvested stands with variable retention along the years after harvesting (3 to 10 years).

	SEE (mill.ha ⁻¹ .year ⁻¹)	REC (n.m ² .year ⁻¹)	EF (%)
3	4.01 ab	8.3 ab	2.12 ab
4	7.20 b	19.2 b	3.96 b
5	3.09 a	11.5 ab	3.53 ab
6	3.01 a	2.2 a	1.62 ab
7	4.74 ab	0.7 a	0.18 a
8	5.10 ab	0.7 a	0.06 a
9	2.34 a	0.3 a	0.08 ab
10	2.57 ab	0.1 a	0.02 a
<i>F(p)</i>	3.14(0.003)	3.91(<0.001)	3.24(0.002)

F = Fisher test; (p) = probability. Different letters showed differences at $p < 0.05$ with Tukey test.

minimum temperature over sea surface during winter (S-MIN-WIN), the average temperature over land surface during summer (T-A-SUM), the maximum temperature over land surface during summer (T-MAX-SUM), and the minimum precipitation during winter (PP-MIN-WIN). The first axis separates the treatments in two groups, primary forests to the left and harvested

stands to the right, while the second axis generates a relative gradient of canopy cover.

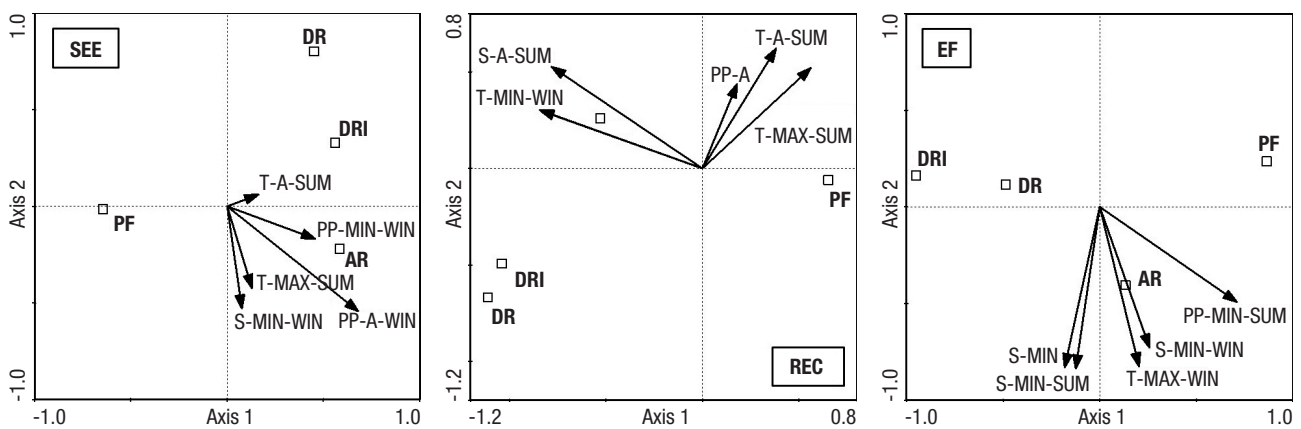
The CCA for seedling recruitment (Table 5 and Figure 1) showed a total inertia of 0.38 (eigenvalue of axis 1 = 0.11 and of axis 2 = 0.02) explaining with both axes 34% of the variation in seedling recruitment by forest types, and 99% of the variation of seedling recruitment by regional climate. The Monte Carlo test presented a $F(p) = 1.32(0.236)$. The climatic variables of higher significance were the minimum temperature of land surface during winter (T-MIN-WIN), the maximum temperature of land surface during summer (T-MAX-SUM), the mean precipitation (PP-A), the average temperature of sea surface during summer (S-A-SUM), and the average temperature of land surface during summer (T-A-SUM). As was observed for seed production, the first axis separates the treatments in primary forests to the right and harvested forests to the left, while the second axis generates a relative gradient of canopy cover.

The CCA for recruitment efficiency (Table 5 and Figure 1) showed a total inertia of 0.43 (eigenvalue of axis 1 = 0.14 and of axis 2 = 0.02) explaining with both axes 39% of the variation in recruitment efficiency by forest types, and 98% of the variation of recruitment efficiency by regional climate. The Monte Carlo test presented a $F(p) = 1.30(0.198)$. The climatic variables of higher significance were the minimum precipitation during summer (PP-MIN-SUM), the minimum temperature of sea surface during winter (S-MIN-WIN), the maximum temperature of land surface during winter (T-MAX-WIN), the minimum temperature of sea surface during summer (S-MIN-SUM) and the minimum average temperature of sea surface (S-MIN). The first axis separates PF and AR (areas with higher canopy cover) from the harvested areas (DRI and DR),

Table 4. ANOVAs for the relative seed production (SEE) (1 = high, 2 = middle, 3 = low production) over recruitment of seedlings (REC) and recruitment efficiency (EF) of the unmanaged primary forests (PF) and harvested stands with variable retention (AR = aggregated retention, DRI = dispersed retention under the aggregate influence, DR = dispersed retention without aggregate influence).

	SEE	REC (n.m ² .year ⁻¹)	EF (%)
PF	1	0.6 a	0.46 a
	2	11.1 a	1.44 ab
	3	51.4 b	2.34 b
	<i>F(p)</i>	20.52(<0.001)	5.63(0.004)
AR	1	1.7	0.97
	2	15.1	2.58
	3	19.4	0.94
	<i>F(p)</i>	1.77(0.175)	1.11(0.333)
DRI	1	1.4	3.09
	2	1.2	0.86
	3	7.0	1.15
	<i>F(p)</i>	2.95(0.056)	0.94(0.393)
DR	1	0.2 a	1.27
	2	1.5 ab	1.30
	3	3.7 b	1.60
	<i>F(p)</i>	3.20(0.044)	0.07(0.929)

F= Fisher test; (p) = probability. Different letters showed differences at $p < 0.05$ with Tukey test.



Codes of climate variables are described in material and methods

Figure 1. Canonical correspondence analysis (CCA) for the seed production (SEE), recruitment of seedlings (REC) and recruitment efficiency (EF) of the unmanaged primary forests (PF) and harvested stands with variable retention (AR = aggregated retention, DRI = dispersed retention under the aggregate influence, DR = dispersed retention without aggregate influence).

whereas the second axis separates AR from the rest of the treatments.

The linear regression fitted for seed production (SEE) explained between 62% and 97% of the variation (Table 6), using average precipitation during winter (PP-A-WIN) and minimum temperature of sea surface

Table 5. Canonical correspondence multivariate analysis of climate variables for the seed production (SEE), recruitment of seedlings (REC) and recruitment efficiency (EF) of the unmanaged primary forests (PF) and harvested stands with variable retention (AR = aggregated retention, DRI = dispersed retention under the aggregate influence, DR = dispersed retention without aggregate influence).

	Variable	U-value	F(p)
SEE	PP-A-WIN	0.05	5.97(0.02)
	S-MIN-WIN	0.03	4.05(0.02)
	T-A-SUM	0.02	3.92(0.03)
	T-MAX-SUM	0.01	1.54(0.19)
	PP-MIN-WIN	0.01	0.52(0.58)
REC	T-MIN-WIN	0.08	5.51(0.01)
	T-MAX-SUM	0.03	2.10(0.11)
	PP-A	0.01	0.57(0.50)
	S-A-SUM	0.01	0.44(0.62)
	T-A-SUM	0.01	0.20(0.77)
EF	PP-MIN-SUM	0.08	4.33(<0.01)
	S-MIN-WIN	0.07	5.06(<0.01)
	T-MAX-WIN	0.01	0.55(0.58)
	S-MIN-SUM	0.01	0.22(0.86)
	S-MIN	0.01	0.22(0.78)

U-value = Wilks Lambda test. F = Fisher test; (p) = probability. Codes of climate variables are described in material and methods.

during winter (S-MIN-WIN) for PF and DRI, while AR also included average temperature of land surface during summer (T-A-SUM). The equation for DR also included PP-A-WIN, and another two different values: minimum precipitation during winter (PP-MIN-WIN) and maximum temperature of land surface during summer (T-MAX-SUM). The fitted models were significant for the four forest types ($p < 0.001$ to 0.035).

The linear regression fitted for seedling recruitment (REC) explained between 55% and 68% of the variation (Table 7), using only minimum temperature of land surface during winter (T-MIN-WIN) for the harvested areas (DR and DRI), and included average temperature of land surface during summer (T-A-SUM) and average precipitation along the year (PP-A) for the areas with higher canopy cover (PF and AR). The fitted models were significant for RDI and RD ($p = 0.023$ and 0.017 , respectively), and marginally significantly for PF and AR ($p = 0.095$ and 0.078 , respectively).

The linear regression fitted for recruitment efficiency (EF) explained between 59% and 95% of the variation (Table 8), using minimum temperature of sea surface during winter (S-MIN-WIN) and summer (S-MIN-SUM) for the primary forests, while the harvested stands using minimum precipitation during summer (PP-MIN-SUM) as main variable, and minimum temperature of sea surface (S-MIN) for AR and DRI, and minimum temperature of sea surface during winter (S-MIN-WIN) for DR. The fitted models were significant for the harvested stands ($p < 0.001$ to 0.006), and marginally significant for PF ($p = 0.109$).

Table 6. Regression models for the seed production (SEE) and the climate variable for the unmanaged primary forests (PF) and harvested stands with variable retention (AR = aggregated retention, DRI = dispersed retention under the aggregate influence, DR = dispersed retention without aggregate influence).

	Variable	Coefficient	(p)	r ² -adj. (%)	EEE (mill.ha ⁻¹ .year ⁻¹)	EMA (mill.ha ⁻¹ .year ⁻¹)
PF	Model		0.035	61.7	9.56	5.28
	PP-A-WIN	-8.302	0.236			
	S-MIN-WIN	20.060	0.186			
AR	Model		0.004	88.4	3.29	2.13
	PP-A-WIN	-3.615	0.158			
	S-MIN-WIN	14.442	0.067			
	T-A-SUM	-3.461	0.277			
DRI	Model		<0.001	97.1	0.56	0.43
	PP-A-WIN	-1.808	0.003			
	S-MIN-WIN	4.478	0.001			
DR	Model		0.003	89.0	0.58	0.44
	PP-A-WIN	-2.452	0.053			
	PP-MIN-WIN	2.578	0.038			
	T-MAX-SUM	0.455	0.247			

(p) = probability. EEE = standard error of estimation. MAE = mean absolute error. Codes of climate variables are described in material and methods.

Table 7. Regression models for the recruitment of seedlings (REC) and the climate variable for the unmanaged primary forests (PF) and harvested stands with variable retention (AR = aggregated retention, DRI = dispersed retention under the aggregate influence, DR = dispersed retention without aggregate influence).

	Variable	Coefficient	(p)	r ² -adj. (%)	EEE (mill.ha ⁻¹ .year ⁻¹)	EMA (mill.ha ⁻¹ .year ⁻¹)
PF	Model		0.095	64.7	29.86	21.69
	T-MIN-WIN	21.312	0.345			
	T-A-SUM	109.621	0.098			
	PP-A	-64.028	0.106			
AR	Model		0.078	68.1	22.35	15.71
	T-MIN-WIN	33.407	0.088			
	T-A-SUM	73.629	0.126			
	PP-A	-45.785	0.118			
DRI	Model		0.023	54.5	5.66	4.50
	T-MIN-WIN	3.350	0.023			
DR	Model		0.017	58.0	2.45	2.01
	T-MIN-WIN	1.560	0.017			

(p) = probability. EEE = standard error of estimation. MAE = mean absolute error. Codes of climate variables are described in material and methods.

Table 8. Regression models for the recruitment efficiency (EF) and the climate variable for the unmanaged primary forests (PF) and harvested stands with variable retention (AR = aggregated retention, DRI = dispersed retention under the aggregate influence, DR = dispersed retention without aggregate influence).

	Variable	Coefficient	(p)	r ² -adj. (%)	EEE (mill.ha ⁻¹ .year ⁻¹)	EMA (mill.ha ⁻¹ .year ⁻¹)
PF	Model		0.109	58.8	1.95	1.41
	S-MIN-WIN	7.850	0.331			
	S-MIN-SUM	-6.445	0.357			
AR	Model		0.001	94.9	0.88	0.62
	PP-MIN-SUM	-2.928	0.003			
	S-MIN	6.925	0.002			
DRI	Model		0.006	90.1	1.42	0.98
	PP-MIN-SUM	-4.351	0.005			
	S-MIN	9.987	0.004			
DR	Model		0.001	92.1	0.93	0.66
	PP-MIN-SUM	-2.558	0.002			
	S-MIN-WIN	6.086	0.001			

(p) = probability. EEE = standard error of estimation. MAE = mean absolute error. Codes of climate variables are described in material and methods.

Discussion

Forest structure and canopy cover

Harvesting significantly modifies the forest structure, and the magnitude of these changes depends on the cutting method (Martínez Pastur *et al.*, 2009; Parker *et al.*, 2013). Variable retention method generates a gradient of changes from the center of the aggregates, where the structure is similar to the primary forest, to the farthest areas in the dispersed retention (Cellini, 2010; Martínez Pastur *et al.*, 2011b). The ag-

gregates maintain some of the natural characteristics of the primary forest (e.g. RLAI) but mostly present intermediate values with the harvested areas. Also, the harvested areas under the influence of the aggregates presented higher values of forest structure than the harvested areas without influence of the aggregates.

Retention levels are directly related with the micro-climatic conditions generated into the forests that were harvested (Chen *et al.*, 1993, 1995), e.g. amount of rainfall that reaches to the forest ground, available radiation under the canopy, wind exposure and temperature (Richter & Frangi, 1992; Caldentey *et al.*, 2005, 2009). These factors had the biggest influences

on growth and survival of natural regeneration in *Nothofagus pumilio* forests (Lieffers *et al.*, 1999; Heinemann *et al.*, 2000; Martínez Pastur *et al.*, 2007, 2011b). However, the influence of the forest structure over regeneration is not linear, e.g. intermediate values of forest cover (45-55%) generate the best conditions for the seedlings growth (Martínez Pastur *et al.*, 2011a). Also, low levels of forest cover generate high light availability, but also generate high contents of soil moisture due to the amount of rainfall, affecting the physiological performance and biomass allocation of seedlings (Lencinas *et al.*, 2007; Martínez Pastur *et al.*, 2007).

Seed production and recruitment

Seed production and recruitment are directly related to the forest cover (Cellini, 2010; Parker *et al.*, 2013), but not to the recruitment efficiency. Some studies suggest that the new stand conditions in the harvested forests were adverse for the seedling recruitment (Collado *et al.*, 2008) but other studies suggest that those conditions improve the establishment and growth (Rosenfeld *et al.*, 2006; Cellini, 2010). In this study, no significant differences were detected in the recruitment efficiency among the studied forest types, where lower values were found in the extreme forest covers (1.39% and 1.46% in DR and PF, respectively) rather than in intermediate covers. This results can indicate better ecological conditions for seedlings, as was previously cited for height growth and eco-physiological performances in plants successfully established (Lencinas *et al.*, 2007; Martínez Pastur *et al.*, 2007, 2011a).

Seed production greatly changed along the years, where the existence of extraordinary seed-falls were observed (e.g. years 4 and 8 after harvesting). This cyclic production of seeds has been cited for many forests species (Kelly, 1994; Kelly *et al.*, 2000; Koenig & Knops, 2000) and was specially described for the *Nothofagus* genera (Monks & Kelly, 2006) due to the high variation levels among years (Kelly, 1994; Kelly & Sork, 2002). However, seedling recruitment and recruitment efficiency values decrease along the years. This decay could be due to changes in the biotic and the abiotic factors of the harvested forests after the cuttings. Among the biotic changes, the dynamic of the understory (e.g. Lencinas *et al.*, 2011; Gallo *et al.*, 2013) and the herbivore grazing (Soler *et al.*, 2012), are the factors with greater influence; and among the abiotic changes, the climate extreme events could be considered as the most influent (e.g. Curran *et al.*, 1999; Schauber *et al.*, 2002; James, 2011). Some studies explored the influence of these factors at stand scale

(microclimate), the seed foraging (e.g. insects, birds and mice) or the relation with seed production (Soler *et al.*, 2013; Martínez Pastur *et al.*, 2013) in *Nothofagus* forests.

Relationships between regional climate with seed production and recruitment

There are different hypothesis that relate some of the seeding processes and climate (Isagi *et al.*, 1997; Liebhold *et al.*, 2004; Bahamonde *et al.*, 2011), however the absence of local climate data in Patagonia did not allow us to determine these relationships. One alternative can be exploring the influence of these factors with the climate at regional scale that was presented and discussed here.

In southern Patagonia Sur, and specially Tierra del Fuego Island, regional climate is controlled by Atlantic Ocean, the influence of the Antarctic climate and Los Andes Mountains, by generating strong climate gradients at regional levels (Kreps *et al.*, 2012). Growing season at these latitudes is restrained to the summer months (Massaccesi *et al.*, 2008; Villalba *et al.*, 2010) and regional climate determined its duration. Also, climate events that occurred during the long winter season influence over summer season, influencing in the ecological conditions of the stands, e.g. higher snow accumulation during winter enlarge ice melting period, increasing the amount of water available in rivers and streams and consequently the availability of water in the forest ground during the summer season (Bales *et al.*, 2011).

The multivariate analyses showed the importance of rainfall over the seed production and recruitment, e.g. the amount of winter rainfall over seed production in the following year, the amount of annual rainfall over the recruitment, and the summer precipitation over the recruitment efficiency. Also, different variables related to winter and summer temperatures were detected as important to predict the observed changes of these variables. For example, minimum winter temperature and summer temperature were related to seed production, summer temperature and minimum winter temperature were related to seedling recruitment in primary and harvested forests, respectively, and minimum temperatures of both seasons were important for the recruitment efficiency. Other studies found similar correlations, e.g. Richardson *et al.* (2005) related seed production of *Nothofagus solandri* with temperature, finding that cold and humid summers produce a higher number of fruits, whereas Smaill *et al.* (2011) also determined the influence of rainfall for the same species. Kon *et al.* (2005) found correlations between

minimum temperatures of the previous spring and seed production of *Fagus crenata* forests, as well as Masaki *et al.* (2008). James (2011) found correlations between growth and recruitment of *Larix sibirica* and *Picea obovata* with fires, land use climate (temperature during different seasons). Finally, Selås *et al.* (2002) found correlations between growth, seed production and climate (temperature and rainfall) in *Picea abies* forests.

Early regeneration of *Nothofagus pumilio* is very sensitive to the lack of soil moisture, mainly during summer season (Heinemann *et al.*, 2000), but when plants growth, the system changes from soil moisture sensitive to light sensitive (Heinemann & Kitzberger, 2006; Martínez Pastur *et al.*, 2011a, 2011b). For this reason, rainfall accumulated during winter or summer rainfall plays a determinant role in seedling recruitment. Also, seedlings are sensitive to ice damage, mainly in environments with low levels of forest cover (e.g. harvested areas) where the occurrence of frost can occur during all the summer season (Martínez Pastur *et al.*, 2009; Kreps *et al.*, 2012).

Some of the studied variables (e.g. seeding patterns) presented cycles that were described for many forest species including *Nothofagus* genera (Monks & Kelly, 2006). This phenomenon occurred both, at regional scale (Kelly, 1994; Kelly & Sork, 2002) and at stand scale (Martínez Pastur *et al.*, 2013; Soler *et al.*, 2013), and probably the first one is correlated with the regional climate, and the second one can be the responsible of the observed variation that can not be explained with the models adjusted here. Beside this, some correlation among the regional climate variables exists, e.g. years with cold winters leads to obtain lower average annual temperatures. These outputs can be taken in account when these models were used.

Conclusions

Forest harvesting modifies the forest structure, but contrasting to other silvicultural proposals, variable retention generates a higher diversity of micro-conditions that influences seed production and seedling recruitment in *Nothofagus pumilio* forests. Seed production and number of recruited seedlings are related to canopy cover, but recruitment efficiency (number of seedlings in relation to number of seeds) is not affected by harvesting. Seed production and recruitment of the different kind of forests (primary forests and harvested stands) are related to regional climate factors and their variations can be explained in the medium term (2006-2013) from variables related to temperature (land and sea surface) and rainfall.

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