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Climate influence seed production in managed and unmanaged *Nothofagus pumilio* forests of Southern Patagonia †

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Abstract

Background: Annual seed production is key to understand natural forest dynamics and to apply sustainable forest management. This process is subjected to variations according to annual and seasonal climatic conditions, locally affected by El Niño-Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) seasonality. Recognising how these variables affect the dynamics of harvested forests is useful for developing forest management strategies. Therefore, the objective of this study was to analyse annual seed production (SP) in *Nothofagus pumilio* (Poepp. & Endl.) Krasser stands harvested under variable retention and unmanaged primary forests in Tierra del Fuego, Argentina, related to the occurrence of climatic events over a 17-year period (2006-2022).

Methods: Seed production (million ha⁻¹ year⁻¹) was annually measured in three managed stands with different retention levels (AR: aggregates; DRI: dispersed with aggregate protection; DR: dispersed without aggregate protection) and three primary forests (PF) stands as control sites (4 treatments x 3 areas x 6 replicates x 17 years). Values of occurrences of climatic events (positive or negative values of ENSO and SAM) were related to monthly temperature and rainfall. ANOVAs, correlation analyses and statistical modelling were performed to predict SP based on climatic variables and forest treatments.

Results: Seed production varied over years and among forest treatments depending on annual climate variations, with annual averages for the studied period of: 9.35 million ha⁻¹ year⁻¹ for PF, 7.16 million ha⁻¹ year⁻¹ for AR, 2.25 million ha⁻¹ year⁻¹ for DRI and 1.08 million ha⁻¹ year⁻¹ for DR. ENSO+ and SAM+ acted as a trigger of high SP, associated to higher temperatures and dry conditions, mainly during spring and summer. The models predicted SP explaining 73-85% of its variability, considering minimum and maximum temperatures and ENSO mean values as better predictors.

Conclusions: Findings presented in this study have important implications for forest management as a tool for understanding forest dynamics related to seeding, a key factor for forest regeneration in a context of high climate variability. However, within a context of climate change with extreme events, there is a need for long-term monitoring of seeding processes in *Nothofagus* forests.

Keywords: seeding; forestry; harvesting; ENSO; SAM; variable retention; forest dynamics; climate drivers; Tierra del Fuego.

Introduction

Forest dynamics around the world are subjected to climate variability, being seeding a critical process for maintaining forest structure over time (Srur et al. 2018; Martínez Pastur et al. 2016; LaMontagne et al. 2020) within a context of climate change (IPCC 2022).

In Tierra del Fuego, Argentina (52° 40' to 55° 03' S, 65° 07' to 68° 36' W), native forests are dominated by *Nothofagus pumilio* (Poepp. & Endl.) Krasser (commonly named lenga), a deciduous species that is naturally distributed in Argentina and Chile from 33° to 56° S (Veblen et al. 1996), growing as natural monospecific formations. This species abundantly regenerates with seeds after natural and human disturbances (e.g., harvesting), following natural dynamics based on gaps openings (Veblen 1989; Alan & Veblen 1993). The proposed management of these monospecific forests is based on the natural regeneration of the harvested stands (Martínez Pastur et al. 2019), by modifying light availability and soil moisture (Martínez Pastur et al. 2009, 2011b), where the remaining canopy overstory acts as a seed source creating favourable microclimatic conditions for seedling growth and survival (Chen et al. 1995, 1999; Martínez Pastur et al. 2011a). Therefore, seeding is an essential process to guarantee forest continuity (Rosenfeld et al. 2006; Martínez Pastur et al. 2011a) and conservation of the natural genetic resources (Marchelli & Gallo 1999; Premoli & Kitzberger 2005) being the first years-after-harvesting (YAH) crucial for seedling recruitment (Martínez Pastur et al. 2011a, 2011b). During the 21st century, variable retention harvesting has been used in *N. pumilio* forests for timber purposes (extracting 30% basal area as aggregates and 15% as dispersed retention), combining economic and conservation objectives (Martínez Pastur et al. 2009, 2019).

Nothofagus pumilio forests concentrate seed fall at the beginning of the autumn with a strong inter-annual variation (Herrera et al. 1998; Torres et al. 2015; Rodríguez-Souilla et al. 2023a). This process is mainly regulated by biological and environmental factors (e.g., topography, soil conditions, and changes in the forest structure) (Hernández et al. 1992; Hackett-Pain et al. 2019; Keyejo et al. 2020), and also influenced by the regional climate during primordia development and flowering (McKee & Richards 1996; Martínez Pastur et al. 2008; Torres et al. 2015). In particular, seeding cycles are well described for other *Nothofagus* forest species (Alley et al. 1998; Monks & Kelly 2006), where the variation over the years (Kelly 1994; Kelly & Sork 2002) depends on forest structure characteristics such as stand basal area, crown cover and site quality (Övergaard et al. 2007; Soler et al. 2010; Bahamonde et al. 2013; Rodríguez-Souilla et al. 2023a). However, silvicultural treatments changes micro-climatic conditions (Promis et al. 2010), increase wind exposure that brings about less flower stability and reduced pollination (Cellini 2010; Toro Manriquez et al. 2016), competition among remnant trees (Martínez Pastur et al. 2008), and changes in nutrient and carbon pool dynamics (Chaves et al.

2023). These factors may exert varying impacts on the diverse silvicultural treatments, which are intricately linked to climate variability (Torres et al. 2015).

Seeding cycles and occurrence of masting events (Piovesan & Adams 2001; Schaubert et al. 2002; Bogdziewicz et al. 2019) depend on physiological and climatic driving factors (Isagi et al. 1997; Liebhold et al. 2004; Bahamonde et al. 2011), particularly during the previous spring and summer (Richardson et al. 2005), but also years prior to seed dispersal (Lowry 1966; Eis 1973). The seed production response of *N. pumilio* to annual climatic variations have been previously reported (Richardson et al. 2005) in Tierra del Fuego (Torres et al. 2015), being strongly affected by both the Atlantic and Pacific oceans, the Antarctic climate, the Andes (Berman et al. 2013; Garreaud et al. 2013), and by large-scale climatic modes such as El Niño-Southern Oscillation (ENSO, with its phases La Niña and El Niño) and the Southern Annular Mode (SAM, with its positive and negative phases) (Silvestri & Vera 2009). Particularly, ENSO (with a periodicity ranging from 2 to 7 years) influences on precipitation patterns in the southernmost regions of South America, on both sides of the Andes Cordillera, particularly through the westerlies (Schneider & Gies 2004). Additionally, SAM exhibits considerable variability, with a decorrelation time of 10 days (Robinson 2000) and two phases characterized by significant seasonal variations (Fogt & Marshall 2020). SAM plays a crucial role in driving temperature and precipitation fluctuations, centered around the intrusion of cold air masses from Antarctica into middle latitudes. The occurrence of ENSO and SAM together (due to the teleconnection phenomena) can amplify climate variability in South America, especially during spring and summer (Silvestri & Vera 2003; Fogt & Bromwich 2006, 2011; Hill et al. 2009; Han et al. 2017; Lim et al. 2019). Besides, the nature of this relationship varies monthly (Vasconsellos et al. 2019). La Niña events tend to promote a positive SAM polarity more frequently, whereas El Niño events are associated with negative SAM polarity. Nonetheless, it is essential to acknowledge that other combinations, resulting from internal variability, may also occur, albeit less frequently (Fogt & Marshall et al. 2020). The utilization of climatic indices such as those developed for ENSO and SAM to comprehend the connections between climate and forest dynamics proves invaluable, especially in regions with limited access to climatic data.

Similarly, Fletcher (2015) demonstrated a distinct correlation between these climatic events and seeding patterns in New Zealand. Furthermore, Rodríguez-Souilla et al. (2023b) applied these indices to assess regeneration height growth, while Srur et al. (2018) employed them to study the establishment of the *N. pumilio* tree line. In this context, the main objective of this study was to explore annual seed production (SP) in *N. pumilio* stands harvested under variable retention compared to unmanaged primary forests at Tierra del Fuego, Argentina, related to the activity of climatic modes over a 17-year period (2006-2022). We address

the following questions:

- (i) Is there a differential response in SP between harvested and primary forests?
- (ii) How does climatic variations brought about by ENSO and SAM activity influence SP over growing seasons? and
- (iii) Is there an interaction between silvicultural treatments and ENSO and SAM?

We hypothesised that climatic events with higher temperatures, especially during flowering and seed formation (spring season) act as a trigger for high SP, finding different responses between treatments due to different microclimatic conditions.

Methods

Study site

The study was conducted in monospecific *Nothofagus pumilio* forests located at Los Cerros Ranch (54°22' S, 67°51' W) in the central area of Tierra del Fuego (Argentina), covering an area of about 2,200 ha. In these forests, variable retention harvesting was implemented for timber production. This harvesting method retains a percentage of the original forest structure by 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 (Martínez Pastur et al. 2009). The studied forests have medium site quality (class II–III according to Martínez Pastur et al. 1997), with dominant tree height of 22–24 m, which presented a range of 700–900 m³ ha⁻¹ of total over-bark volume and 70–80 m² ha⁻¹ of basal area before harvesting. This study frames within the long-term PEBANPA network of permanent sample plots (Parcelas de Ecología y Biodiversidad de Ambientes Naturales en Patagonia Austral, INTA-UNPA-CONICET, Argentina) (Peri et al. 2016).

Sampling design

Six stands (5–20 ha each) were selected for measurements at Los Cerros Ranch (Figure 1): three stands were harvested with variable retention, while three stands of undisturbed forests were considered as control (primary unmanaged forests, PF). Within the harvested stands, sampling plots were randomly located covering three different conditions according to the retention levels (see Martínez Pastur et al. 2011a): (i) within aggregate retention (AR) supposed not to present harvest effects, (ii) dispersed retention under the influence of AR (<20 m from the aggregate edges) (DRI), and (iii) dispersed retention outside the influence of AR (DR). A total of 72 sampling plots were selected (3 managed stands × 3 treatments × 6 plots, plus 3 primary forest stands × 6 plots), and monitored annually between 2006 and 2022 (Figure 1). Rodríguez-Souilla et al. (2023a) showed for the same experiment and time period, significant differences for stand variables among silvicultural treatments and time periods.

Stand basal area averaged 71.4 m² ha⁻¹ for PF, 60.4 m² ha⁻¹ for AR, 16.9 m² ha⁻¹ for DRI and 8.8 m² ha⁻¹ for DR, while canopy cover averaged 86.6% for PF, 74.8% for AR, 48.9% for DRI and 40.2% for DR (Figure 2).

Litter traps (50 × 30 × 20 cm hard plastic baskets) were randomly placed in each plot within control and harvested stands, which were kept in their fixed locations throughout the monitored years, protected with sticks around them to reduce the possibility of disturbance by livestock. Each trap was collected every May and manually sorted in seeds and leaves of *N. pumilio* trees; other components of the litter were discarded (e.g., small branches, fungi, epiphyte plants, miscellaneous, and other understory species). The reason to collect litterfall in May follows the results of Martínez Pastur et al. (2008), who found that most of the seeds fall between March and April, and 90% of the leaves during April. Seeds were counted, and production at each sampling area was quantified (SP, million ha⁻¹ year⁻¹).

Regional climate data

Climatic data was obtained from the ERA5 (Hersbach et al. 2020) grid corresponding to the studied area during 30 years (1993–2022): mean, minimum and maximum monthly air temperatures (T^o = mean temperature, T^o MIN = minimum temperature, T^o MAX = maximum temperature) and monthly accumulated precipitations (PP = rainfall). For our purposes, climatic data were aggregated by season (WIN = winter, July–September; SPR = spring, October–December; SUM = summer, January–March; GS = full growing season, October–March), in order to capture the potential seasonal variations in climate patterns related to tree phenology. For the codes used for climatic variables see the list of abbreviations.

The years covering the post-harvest period (2006–2022) were characterised through the oscillation of occurrence of hemispheric modes (ENSO and SAM, in their joint behaviour) in order to assess their influence over seeding (divided in the season periods mentioned before). Values of ENSO (Southern Oscillation Index - SOI) and SAM (Marshall 2003) were obtained from open-access data (<https://www.weather.gov/fwd/indices> and <https://stateoftheocean.osmc.noaa.gov/atm/sam.php>). Each period was classified according to its prevalence as positive (+) or negative (-) ENSO-SAM values (ENSO-/SAM-, ENSO+/SAM-, ENSO-/SAM+, ENSO+/SAM+). Positive and negative ENSO values represent La Niña or El Niño events, for cold and warm phases at tropical latitudes, respectively. Positive SAM values indicate the contraction of the westerly wind belt towards Antarctica, whereas negative values signify its northward expansion.

The period 2006–2022 showed anomalies compared to the period 1993–2022. Air temperatures anomalies were +0.13 °C for winter, +0.17 °C for spring, and +0.17 °C for summer. Precipitation anomalies were -17 mm for winter, +10 mm for spring, while summer did not exhibit anomalies. The years and seasons with the highest temperature anomalies were: winters 2011, 2017 and 2021 (-0.81 °C, +1.43 °C, +1.35 °C), spring 2009,

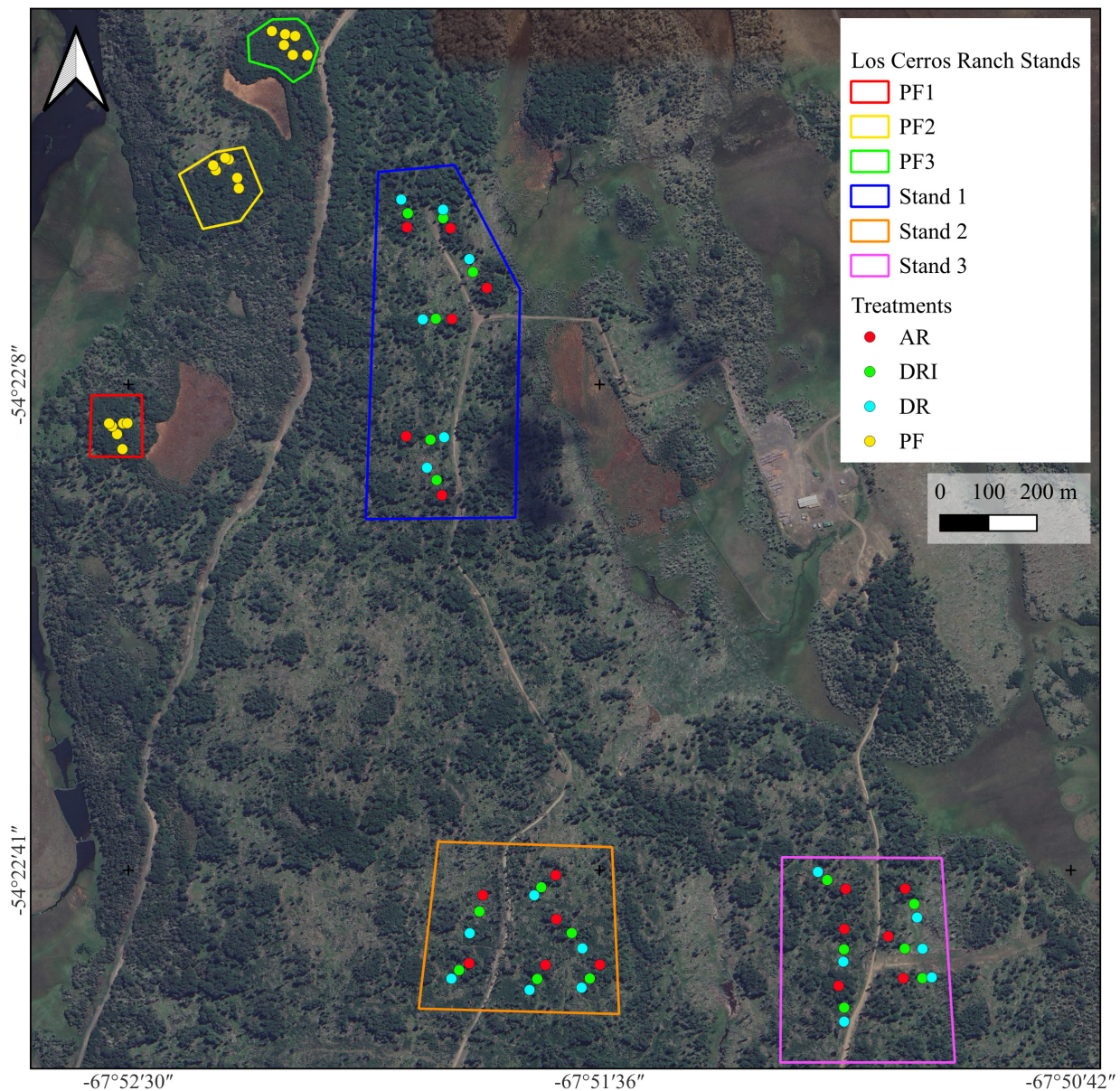


FIGURE 1: Locations of sampling sites. Primary forests (PF) and treatments (AR= aggregated retention, DRI = dispersed retention under the influence of AR, DR = dispersed retention outside the influence of AR).

2020 and 2022 (-0.98°C, +0.73 °C, +1.95 °C), summers 2014 and 2021 (-1.01 °C, +1.06 °C). Precipitation anomalies were observed for: winters 2009 and 2020 (+56 mm, -23 mm), springs 2011, 2015, and 2019 (-74 mm, -75 mm, +25 mm) and summers 2010, 2014, and 2021 (+45 mm, +46 mm, -39 mm).

Statistical analyses

Relationships among the 24 climatic variables and SP for each forest treatments (PF, AR, DRI, DR) were estimated by applying Pearson correlation ($p < 0.05$). For that, ENSO and SAM average values for each season were considered. Then, univariate analyses were performed for comparisons. Different analyses of variance (ANOVA) were conducted, applying independent analyses sequentially to account for time-dependence of the data:

- (i) 17 one-way ANOVAs to analyse SP for each year of the studied period considering forest treatments as main factors;
- (ii) two-way ANOVAs to analyse temperatures and rainfalls values considering ENSO and SAM as main factors during the studied seasons;
- (iii) 6 one-way ANOVAs to analyse climatic factors (2: temperatures and rainfall values) considering ENSO and SAM as main factors during the studied seasons (3: winter, spring and summer); and
- (iv) 12 two-way ANOVAs to analyse SP considering ENSO and SAM as main factors for each forest treatments (4: PF, AR, DRI, DR) during the studied seasons (3: winter, spring and summer).

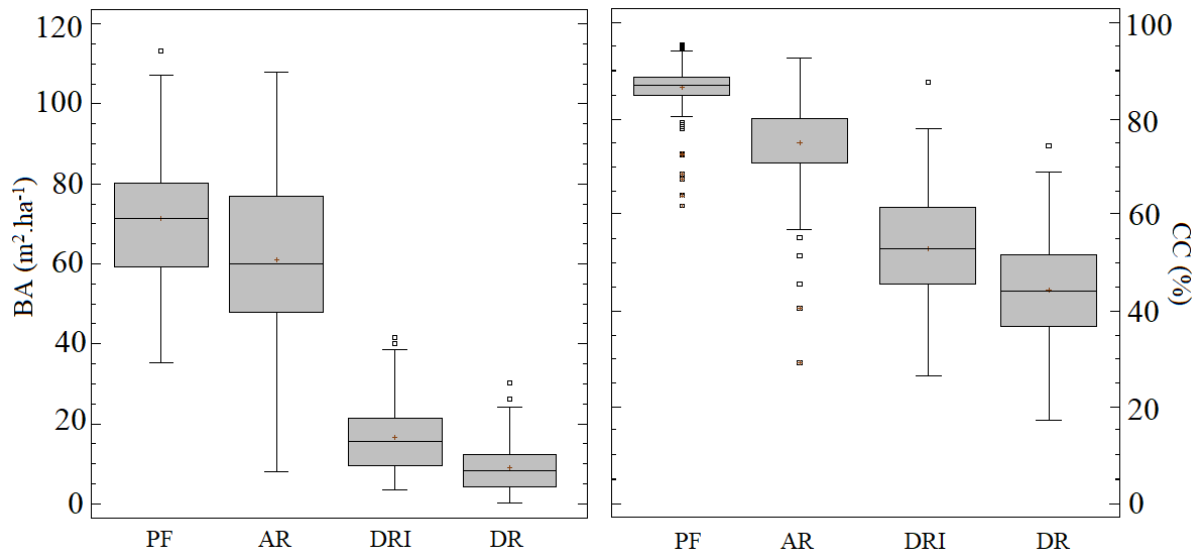


FIGURE 2: Boxplot for basal area (BA, m² ha⁻¹) and crown cover (CC, %) in the different forest treatments (PF = primary forests, AR = aggregated retention, DRI = dispersed retention under the influence of AR, DR = dispersed retention without influence of AR).

Data were tested for normality using the Shapiro-Wilk test, and log transformations were applied when needed. Differences among means were compared using Tukey test ($p < 0.05$). Most significant explanatory variables of SP were found preliminary using Pearson correlation. Linear models of SP by forest type (PF, AR, DRI, DR) were then fitted to climatic data (temperature and rainfall) and also SAM or ENSO mean values. To assess goodness of fit, r^2 -adjusted, p -values, standard error of the estimation (SEE), and mean absolute error (MAE) were calculated using Statgraphics Centurion software (StatPoint, USA).

Results

Annual seed production

Seed production annually varied with high (e.g., 2009, 2012, 2019, 2022) and low values (e.g., 2010, 2014, 2020) (Figure 3). The average SP of the studied period was 9.35 million ha⁻¹ year⁻¹ for PF, 7.16 million ha⁻¹ year⁻¹ for AR, 2.25 million ha⁻¹ year⁻¹ for DRI and 1.08 million ha⁻¹ year⁻¹ for DR. All treatments showed a similar pattern, being in the order PF>AR>DRI>DR, except for some exceptional years when AR>PF (e.g., 2011 and 2017). Treatments showed significant SP differences

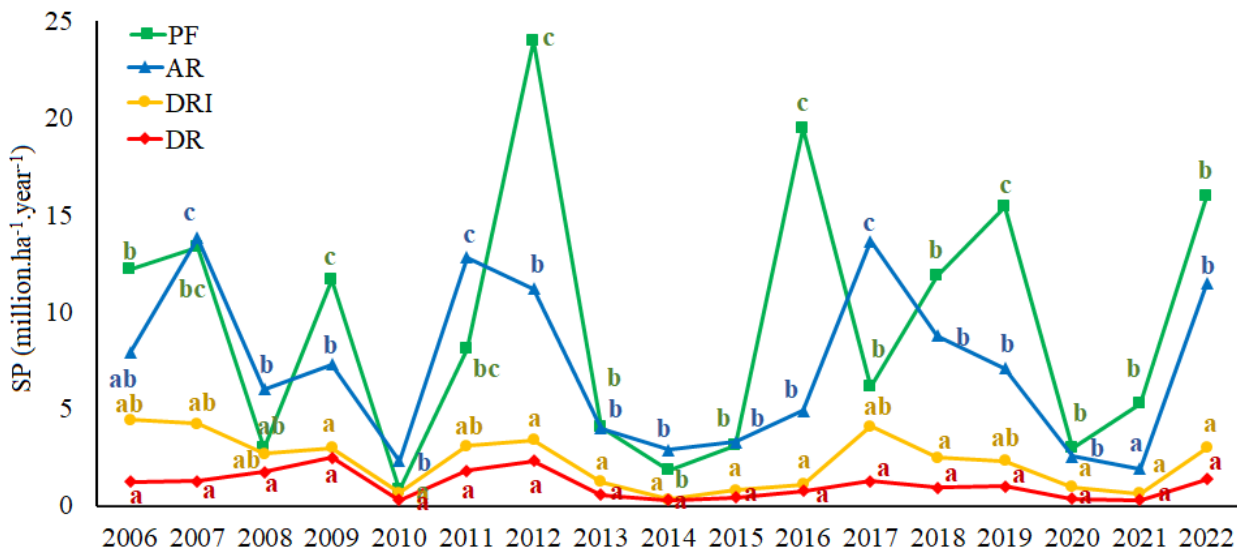


FIGURE 3: Annual seed production (million ha⁻¹ year⁻¹) observed over the studied period (2006-2022) in the different forest treatments (PF = primary forests, AR = aggregated retention, DRI = dispersed retention under the influence of AR, DR = dispersed retention without influence of AR). One-way ANOVAs were conducted to evaluate differences in SP among treatments for each year (see Appendix). Letters show significant differences for each single year between forest treatments using Tukey test at $p < 0.05$.

mainly between PF and AR when compared with DRI and DR (except 2021, where AR did not differ between retention levels).

Climate characterisation

Mean temperature values showed significant differences only for T°WIN ($p = 0.018$), being warmer for ENSO+ (Table 1). SAM+ was related to higher temperatures. Interaction did not occur for T° SPR. Similar trends occurred for minimum and maximum temperatures, with significant interactions for T° MAX SPR ($p = 0.022$) and T° MIN WIN ($p = 0.023$) (Table 2). On the other hand, rainfall showed significant differences for the different SAM events, particularly for SPR and SUM, where SAM- showed higher values.

ENSO/SAM significantly changed mean temperatures and accumulated rainfall depending on time of the year (Figure 4). Regarding temperatures, ENSO+/SAM+ winters were related to warmer values. In spring, ENSO-/SAM- showed higher values, followed by ENSO+/SAM- and ENSO+/SAM+. During the summer, the lowest temperatures were recorded in ENSO-/SAM-. Regarding rainfall, only the combinations with SAM- showed higher rainfall during winter and summer.

Seed production related to climate

There were significant correlations between climatic variables and SP for the studied treatments (Table 3). For example, rainfall (PP SUM and PP GS) only correlated negatively with SP in PF (-0.34 and -0.36 respectively). Minimum and maximum temperatures (T° MIN SPR, T° MIN SUM, T° MAX SPR) showed positive (negative) correlations with maximum (minimum) temperatures

across all treatments. ENSO and SAM showed both positive correlations with SP, especially for spring and summer. PF was the treatment that, on average, showed the highest Pearson values related to climatic variables.

Annual seed production varied according to seasonal climate and silvicultural treatment (Figure 5). SP in PF drastically changed with ENSO/SAM values for spring and summer, finding that the combination ENSO+/SAM+ triggers more SP, followed by ENSO-/SAM+, while during winter ENSO-/SAM- seed production was reduced. On the other hand, SP for AR did show significant differences during winter, with SP being favoured by ENSO+/SAM+. During spring and summer, ENSO+/SAM+ also presented high values for SP, although ENSO+/SAM- became more prominent during summer. DRI and DR showed similar patterns of SP, showing the highest values during winter and spring occurring ENSO+/SAM+ and ENSO-/SAM-, but not in summer, where, similar to AR, ENSO+/SAM- was the one that presented highest SP.

The multiple regression models that best fitted SP (2 models \times 4 treatments = 8) had an r^2 -adj. between 73.2% and 85.2% (Table 4). Main trends showed that the equations included minimum and maximum winter and summer temperatures (PF, DRI and DR), as well as mean spring temperature (AR, DRI, DR). When incorporating ENSO and SAM values, ENSO SPR and ENSO GS prevailed.

Discussion

Our results showed interannual variation in SP for *N. pumilio* forests (Cellini 2010; Rodríguez-Souilla et al. 2023a) with an approximate 3-year cycle occurrence of high seed production pulses that seems enough to

TABLE 1: Two-way ANOVA to test differences in mean temperature and accumulated precipitation (see codes on List of abbreviations), considering positive (+) and negative (-) ENSO and SAM seasonal occurrence as main factors. Different letters indicated significant differences using Tukey test at $p < 0.05$. F = Fisher test, p = probability.

Index		T° GS	T° WIN	T° SPR	T° SUM
A = ENSO	+	7.03	2.42 b	5.86	7.78
	-	6.82	1.87 a	6.03	7.86
	F (p)	0.99 (0.329)	6.28 (0.018)	0.85 (0.363)	0.08 (0.783)

B = SAM	+	6.87	2.32	6.04	7.95
	-	6.98	1.98	5.85	7.70
	F (p)	0.23 (0.636)	2.36 (0.136)	1.01 (0.325)	0.84 (0.367)
A x B	F (p)	0.01 (0.940)	0.64 (0.429)	4.86 (0.036)	0.01 (0.937)

Index		PP GS	PP WIN	PP SPR	PP SUM
A = ENSO	+	597.16	109.98	177.64	197.52
	-	602.03	114.87	161.06	178.85
	F (p)	0.05 (0.827)	0.25 (0.618)	2.04 (0.165)	1.29 (0.265)

B = SAM	+	553.03 a	118.24	147.59 a	160.61 a
	-	646.14 b	106.30	191.10 b	216.76 b
	F (p)	18.01 (0.001)	1.59 (0.218)	14.02 (0.001)	13.03 (0.001)
A x B	F (p)	0.13 (0.719)	0.30 (0.594)	0.38 (0.545)	0.10 (0.750)

TABLE 2: Two-way ANOVA to test differences in mean minimum and maximum temperature (see codes on List of Abbreviations), considering positive (+) and negative (-) ENSO and SAM seasonal occurrence as main factors. Different letters indicated significant differences using Tukey test at $p < 0.05$. F = Fisher test, p = probability.

Index		T° MAX GS	T° MAX WIN	T° MAX SPR	T° MAX SUM
A= ENSO	+	11.39	7.84	10.13	12.14
	-	11.28	7.73	10.43	12.40
	F (p)	0.23 (0.636)	1.53 (0.226)	2.17 (0.540)	0.87 (0.359)
B= SAM	+	11.33	7.88 b	10.44	12.53
	-	11.34	7.69 a	10.11	12.02
	F (p)	0.01 (0.990)	4.28 (0.048)	2.69 (0.113)	3.37 (0.077)
AxB	F (p)	0.53 (0.475)	0.77 (0.388)	5.89 (0.022)	0.20 (0.656)
Index		T° MIN GS	T° MIN WIN	T° MIN SPR	T° MIN SUM
A= ENSO	+	0.75	-2.08	-0.91	1.43
	-	0.66	-2.37	-1.04	1.31
	F (p)	0.31 (0.583)	1.21 (0.281)	0.60 (0.444)	0.67 (0.420)
B= SAM	+	0.73	-1.97	-0.85	1.40
	-	0.68	-2.47	-1.09	1.35
	F (p)	0.11 (0.746)	3.68 (0.065)	2.09 (0.160)	0.09 (0.76)
AxB	F (p)	0.50 (0.487)	5.88 (0.023)	0.05 (0.823)	0.77 (0.387)

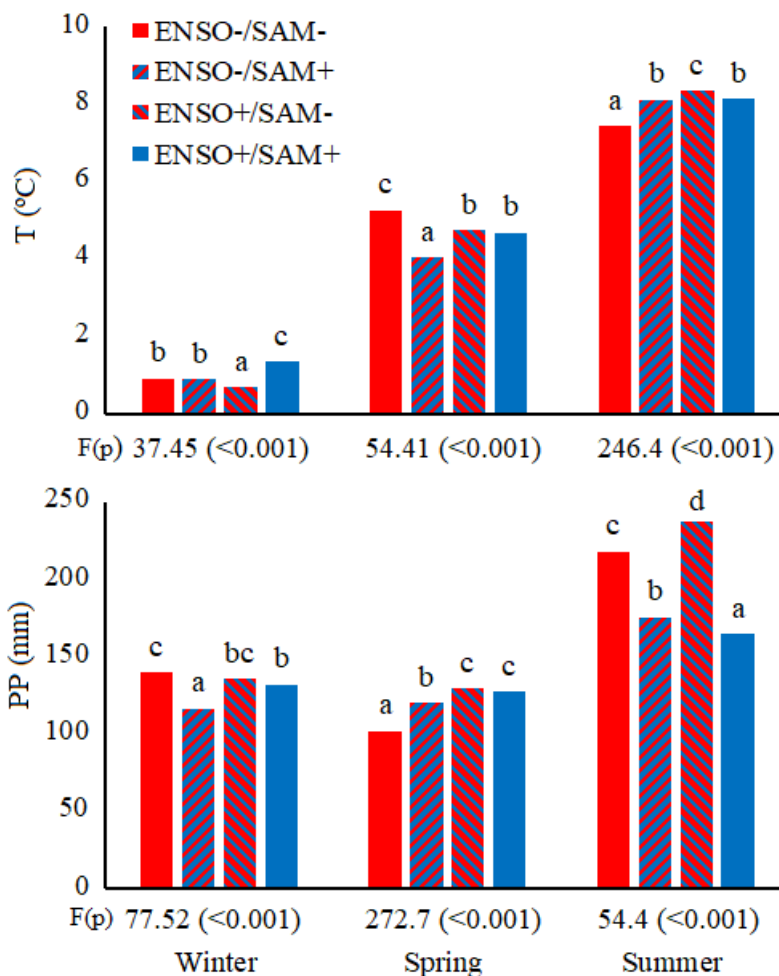


FIGURE 4: (top) Mean air temperature (°C) and accumulated rainfall (mm during period; bottom) for each season (winter, July-September; spring, October-December; summer, January-March) considering years 1993 to 2022. One-way ANOVAs were conducted to evaluate differences. Letters show significant differences between ENSO and SAM seasonal combination using Tukey test at $p < 0.05$.

TABLE 3: Pearson correlation coefficient (PC) and p-value (p) for seed production for each forest treatment (PF = primary forests, AR = aggregated retention, DRI = dispersed retention under the influence of AR, DR = dispersed retention without influence of AR) against different climatic variables (see codes on List of Abbreviations). Significant p values are highlighted in bold.

Climate variable	PF		AR		DRI		DR	
	PC	p	PC	p	PC	p	PC	p
PP WIN	0.04	0.549	0.01	0.918	-0.01	0.828	-0.09	0.146
PP SPR	0.01	0.883	0.03	0.660	0.12	0.050	0.13	0.033
PP SUM	-0.34	<0.001	0.07	0.270	0.04	0.480	-0.07	0.228
PP GS	-0.36	<0.001	0.02	0.769	0.02	0.699	-0.07	0.224
T° WIN	-0.14	0.015	0.05	0.395	-0.03	0.631	-0.07	0.236
T° SPR	0.12	0.036	0.21	0.001	0.10	0.101	0.11	0.077
T° SUM	0.12	0.035	0.01	0.887	0.01	0.826	0.06	0.358
T° GS	-0.14	0.014	-0.03	0.579	-0.09	0.152	-0.08	0.179
T° MIN WIN	0.12	0.047	0.03	0.616	-0.03	0.587	-0.01	0.819
T° MIN SPR	-0.20	0.001	-0.08	0.171	-0.10	0.083	-0.09	0.143
T° MIN SUM	-0.20	0.001	-0.12	0.045	-0.20	0.001	-0.18	0.004
T° MIN GS	0.00	0.982	0.03	0.611	-0.04	0.524	-0.03	0.611
T° MAX WIN	0.01	0.931	0.05	0.384	-0.03	0.611	-0.02	0.699
T° MAX SPR	0.27	<0.001	0.24	0.001	0.14	0.024	0.14	0.017
T° MAX SUM	0.28	<0.001	-0.01	0.875	0.00	0.939	0.05	0.421
T° MAX GS	0.24	<0.001	-0.04	0.455	-0.07	0.273	-0.03	0.650
ENSO WIN	0.03	0.600	0.28	<0.001	0.17	0.004	0.19	0.001
ENSO SPR	0.29	<0.001	0.29	<0.001	0.23	0.001	0.31	<0.001
ENSO SUM	0.08	0.182	0.21	0.001	0.17	0.004	0.25	<0.001
ENSO GS	0.13	0.025	0.24	<0.001	0.18	0.003	0.25	<0.001
SAM WIN	0.29	<0.001	0.23	0.001	0.17	0.004	0.18	0.003
SAM SPR	0.32	<0.001	0.18	0.003	0.17	0.005	0.20	0.001
SAM SUM	0.18	0.002	-0.17	0.004	-0.10	0.108	0.01	0.903
SAM GS	0.42	<0.001	0.20	0.001	0.17	0.004	0.25	<0.001

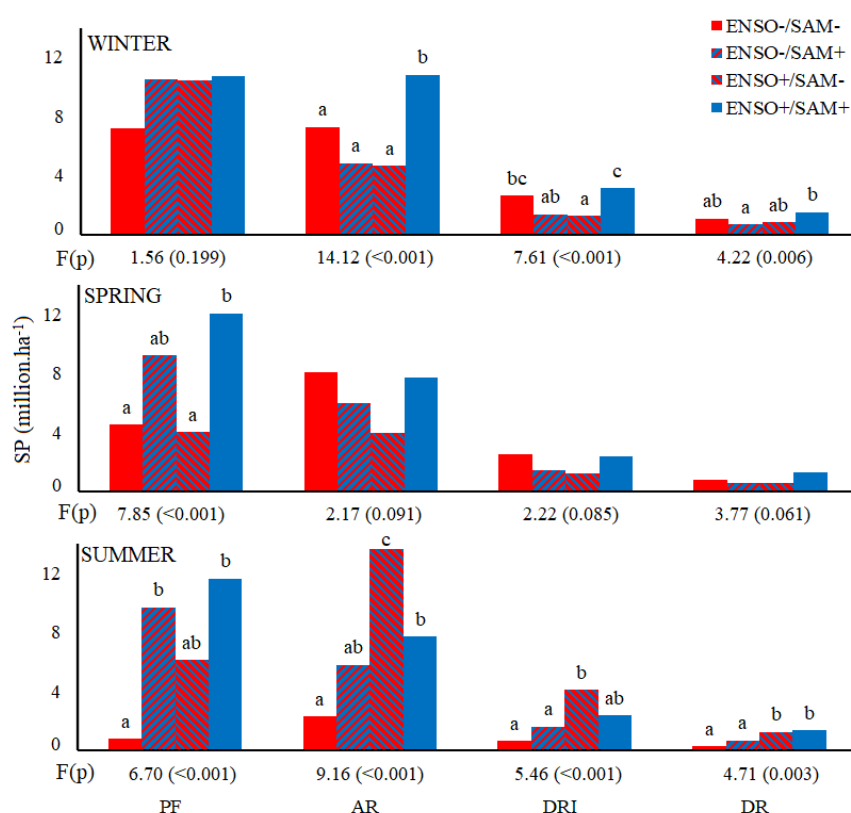


FIGURE 5: Mean annual seed production (SP, million ha⁻¹ year⁻¹), for each forest treatment (PF = primary forests, AR = aggregated retention, DRI = dispersed retention under the influence of AR, DR = dispersed retention without influence of AR) considering ENSO-SAM combination occurrence during each season (winter, July-September; spring, October-December; summer, January-March). One-way ANOVA were conducted to evaluate differences. Letters show significant differences for each single graph among ENSO-SAM combinations using Tukey test at p < 0.05.

TABLE 4: Regression models for annual seed production and climatic variables (codes on List of Abbreviations) for each forest treatment (PF = primary forests, AR = aggregated retention, DRI = dispersed retention under the influence of AR, DR = dispersed retention without influence of AR). p = probability, r^2 -adj = coefficient of determination. SEE = standard error of estimation (million ha⁻¹ year⁻¹), MAE = mean absolute error (million ha⁻¹ year⁻¹).

Treatment	Variables	Coefficient	p	r^2 -adj. (%)	SEE	MAE
PF	Model		<0.001	81.6	4.530	3.422
	T MIN WIN	12.658	<0.001			
	T MIN SUM	-28.515	<0.001			
	T MAX SUM	2.372	0.031			
PF	Model		<0.001	79.3	6.677	4.902
	PP GS	0.058	<0.001			
	ENSO GS	-4.694	<0.001			
	ENSO WIN	1.518	0.002			
	ENSO SPR	3.328	<0.001			
AR	Model		0.001	81.8	2.925	2.439
	T SPR	4.756	<0.001			
	T GS	-8.429	<0.001			
	T MAX WIN	3.261	0.003			
AR	Model		<0.001	85.2	2.635	2.070
	PP SPRI	0.04	<0.001			
	SAM WIN	1.877	<0.001			
	ENSO GS	0.174	<0.001			
DRI	Model		<0.001	83.9	1.058	0.795
	T MIN SUM	-3.623	<0.001			
	T SPR	1.607	<0.001			
DRI	Model		<0.001	73.2	1.231	0.955
	T SPR	0.395	<0.001			
	ENSO SPR	0.043	0.031			
DR	Model		<0.001	75.5	0.514	0.390
	T MAX SUM	3.658	<0.001			
	T GS	-4.454	<0.001			
	T SPR	3.935	<0.001			
DR	Model		<0.001	74.8	0.822	0.613
	ENSO GS	-0.103	0.024			
	ENSO SPR	0.135	0.001			
	T MIN SPR	-1.005	<0.001			

regenerate at full density managed stands (Martinez Pastur et al. 2009, Rodríguez-Souilla et al. 2023b). We showed that climate affects annual seed production, as shown in Table 3 and Figure 5. This could be explained by differences in the allocation of resources at different times of the year (e.g. carbon and other nutrients), as well as differences in growing season length and modification of tree phenological stages (Torres et al. 2015; Bogdziewicz et al. 2019). In our study, warm springs may lead to more uniform and abundant flowering and pollination success (Allen & Plat 1990), and therefore higher SP, associated to the critical phase of floral primordial development (Schauber et al. 2002;

Martinez Pastur et al. 2007). In addition, warmer temperatures during spring (primordia development and flowering) and summer (seed formation) would drive greater net carbon uptake (Allen & Plat 1990; Richardson et al. 2005). Although further studies are needed to extrapolate these relationships to a larger geographical scale, the results obtained are consistent with the hypothesis proposed in this study. Thus, minimum and maximum temperatures explained SP, having a negative effect for minimum temperature and a positive effect for maximum temperatures, especially during spring and summer seasons, as was reported by Torres et al. (2015).

The seasonal influence of simultaneous ENSO and SAM events on SP has also been demonstrated in the present study, where growing season was restrained to the summer months (Villalba et al. 2010) and regional climate determined its duration. In consonance with climatic variables (T° and PP), ENSO+ and SAM+ events tend to favour high SP for *N. pumilio* forests. This is consistent with Srur et al. (2018) who reported that higher temperatures may generate greater seedling abundance and growth. Also, the effects of ENSO and SAM on physiological processes in different forests has been reported (Schauber et al. 2002; Hadad et al. 2021), being modified according to how their seasonality in temperature and rainfall affect different parts of the world. Besides, studies have reported that higher temperatures associated to low rainfalls are correlated with years of high SP, especially during the spring (e.g., flowering time reported by McKee & Richards 1996; Buechling et al. 2016; Gallego Zamorano et al. 2018). Low winter temperatures can extend the dormant season, therefore limiting physiological processes that affect annual flowering development (Fritts 1976), soil nutrient acquisition (Smaill et al. 2011), which in turn reduces SP.

The main differences in SP between treatments occurred between PF and harvested treatments (AR presented mixed effects compared to other treatments). This is likely due to the microclimatic conditions generated in harvested stands (Chen et al. 1999; Martinez Pastur et al. 2007; Rodríguez-Souilla et al. 2023a) by altering flowering and fruiting of the remaining trees (Rodríguez-Souilla et al. 2024). In turn, the models obtained in this study can account for the influence (positive or negative) of climatic variables on SP, including ENSO and SAM indices to improve predictions. While rainfalls were not a limiting factor for SP, temperatures (mainly for harvested) in SAM events play a forcing role on its variability. So, SP in PF was influenced by the growing season accumulated precipitation, effect also reported by Smaill et al. (2011) for *Nothofagus solandri* var. *cliffortioides* forests

In the context of climate change with periodic increases in temperature and variations in annual rainfall (IPCC 2022) and the occurrence of climatic extreme events, it is likely that annual seed production could be altered (Monks et al. 2016). In addition, the cycle and frequency of masting events for *Nothofagus* forests (detected only for the year 2012 in this work) might be modified under climate change conditions (Cuevas 2000, 2002; Övergaard et al. 2007), although it may be insensitive to increases in global mean temperature (Kelly et al. 2013; Hackett-Pain & Bogdziewicz 2021), where constant heavy flowering or desynchronization may happen. The findings presented in this study may have important implications for forest management as a tool for understanding forest dynamics related to seeding, a key process for forest regeneration (Rodríguez-Souilla et al. 2023b) in a context of high climate variability.

Conclusions

Seed production of *N. pumilio* had a great variability along 17 years of evaluation, being annual climate variations a key factor that influenced the response between forest treatments. In particular, ENSO and SAM effects on regional climate (especially ENSO+ and SAM+) determined climate variability (mainly minimum and maximum temperatures). Although seed production tended to decrease along the period studied, values reported seem to be sufficient for forest regeneration. In the context of climate change, there is a need for long-term monitoring of seeding process and other forest dynamics characteristics over different *Nothofagus* forests for conservation and economic purposes.

List of abbreviations

PP WIN: accumulated winter rainfall (mm)
 PP SPR: accumulated spring rainfall (mm)
 PP SUM: accumulated summer rainfall (mm)
 PP GS: accumulated growth season rainfall (mm)
 T° WIN: average winter temperature ($^{\circ}$ C)
 T° SPR: average spring temperature ($^{\circ}$ C)
 T° SUM: average summer temperature ($^{\circ}$ C)
 T° GS: average growth season temperature ($^{\circ}$ C)
 T° MIN WIN: average minimum winter temperature ($^{\circ}$ C)
 T° MIN SPR: average minimum spring temperature ($^{\circ}$ C)
 T° MIN SUM: average minimum summer temperature ($^{\circ}$ C)
 T° MIN GS: average minimum growth-season temperature ($^{\circ}$ C)
 T° MAX WIN: average maximum winter temperature ($^{\circ}$ C)
 T° MAX SPR: average maximum spring temperature ($^{\circ}$ C)
 T° MAX SUM: average maximum summer temperature ($^{\circ}$ C)
 T° MAX GS: average maximum growth-season temperature ($^{\circ}$ C)
 ENSO WIN: winter ENSO
 ENSO SPR: spring ENSO
 ENSO SUM: summer ENSO
 ENSO GS: growth season ENSO
 SAM WIN: winter SAM
 SAM SPR: spring SAM
 SAM SUM: summer SAM
 SAM GS: growth season SAM

Competing interests

The authors declare they have no conflicting interests.

Authors' contributions

GMP and PLP conceived and designed the experiments, MVL, JMC, JEC and JRS collaborated in fieldwork and data analysis, and FAR helped in writing the manuscript. All authors have read and agreed to the published version of the manuscript.

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