

## Article

# Microclimatic Conditions Restrict the Radial Growth of *Nothofagus antarctica* Regeneration Based on the Type of Forest Environment in Tierra del Fuego

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**Abstract:** Regeneration is crucial for forest continuity in natural and managed stands. Analyzing intra-annual dynamics can improve the understanding between growth and climate, identifying regeneration survival thresholds. The objective of this study was to determine the microclimate constraints (rainfall, air, and soil temperatures) of *Nothofagus antarctica* regeneration growth in closed, open, and edge forests in Southern Patagonia. We measured stand characteristics (forest structure, understory plants, soil properties, animal use), microclimate, and the daily growth of regeneration using dendrometers ( $n = 6$ ) during two growing seasons. We found significant differences in the studied variables (e.g., overstory, light, soil, understory plants, animal use) in the following order: closed primary forests > open forests > edge forests with openlands. These changes defined the microclimate across the overstory gradient (e.g., soil moisture), influencing the daily growth of regeneration across the growing season (lag, exponential, stationary). Rainfall (the F factor varied from 6.93 to 21.03) influenced more than temperature (the F factor varied from 0.03 to 0.34). Daily growth in closed forests indicated shrinkage ( $-0.0082 \text{ mm day}^{-1}$  without rain and  $-0.0008 \text{ mm day}^{-1}$  with  $0.0\text{--}0.2 \text{ mm day}^{-1}$  rainfall), while for more than  $0.2 \text{ mm day}^{-1}$  of rainfall, growth always increased. Open forests presented shrinkage during days without rain ( $-0.0051 \text{ mm day}^{-1}$ ), showing positive growth according to rainfall. Edge forests always presented positive daily growth. The resilience of regeneration under these changed conditions was directly related to the overstory. The main outputs indicated that regeneration was vulnerable during non-rainy days at the middle or closed overstory (>40% crown cover), suggesting the need for long-term monitoring to develop better silvicultural proposals.

**Keywords:** silvopastoral systems; regeneration growth; daily stem dynamics; dendrometers; microclimate; soil water content

## 1. Introduction

The forest structure of native forest stands changes across the landscape according to species ecology, climate, topography, and disturbance regimes (e.g., windstorms) [1]. At

high latitudes, temperate native forests show simple horizontal and vertical structures, usually with few dominant species and with one or two overstory strata, following predictable forest dynamic paths. For example, *Nothofagus antarctica* (Forst. f.) Øerst. (commonly called ñire) forests in Tierra del Fuego (Argentina) grow in pure stands and regenerate from seeds or root sprouts under simple gap dynamics [2,3]. A silvopastoral system was proposed to manage these forests, where the main provisional monetary services are firewood (ranch consumption) and livestock (e.g., sheep and cattle grazing). *Nothofagus antarctica* forests concentrate the cattle breeding of Tierra del Fuego, which is the main income source of ranching activities [2]. This management proposal simplifies the forest structure by opening the canopy through thinning, maintaining homogeneous tree and age distributions [4], and promoting an increase in understory biomass [5,6] for livestock production [7,8]. Forest structure values (e.g., volume, growth, and forest regeneration) have been previously studied [3,9], and several constraints during the management cycle may affect the natural regeneration of stands [8,10].

In *Nothofagus* forests, regeneration survival and growth are crucial to maintaining the forest cover continuity over time [11]. The main variables that influence regeneration performance are the microclimate (e.g., light and water availability) regulated by the forest overstory cover [12] and other biotic factors such as animal browsing (e.g., natural populations of *Lama guanicoe* or domestic livestock) [8,13]. Furthermore, harvesting modifies the forest structure by altering ecosystem functions, microclimates, and natural cycles depending on cut intensity [3]; e.g., thinning stimulates seedling growth by modifying light availability and soil moisture, and the remaining canopy overstory acts as a seed source and mitigates microclimatic conditions inside the harvested stands [4,14].

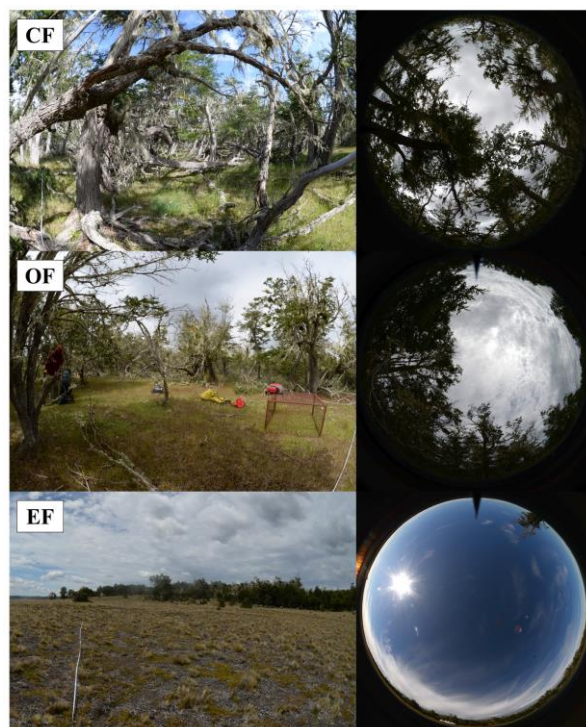
These relationships with natural regeneration, forest structure, and climate have been described before for different seasons [15]; however, the impact on the tree-ring formation period is still uncertain. At higher latitudes, the tree ring is developed in a short period of time (e.g., three months per year) [16], strongly depending on daily climate conditions, which greatly impact the growth performance [17,18]. Microclimatic conditions change between the different forest environments, and some stands are more resilient to extreme climatic events, e.g., reducing the impact of low or high temperatures and drought or freezing events [3,14,19,20]. Tree growth responses (increases or decreases in diameter) and the mechanisms that drive productivity across the growing season depend on daily microclimatic conditions [21,22]. Understanding the relationships between tree-ring formation and the climate can improve the knowledge of growth dynamics (e.g., dendrochronological studies) [23–25] and the survival thresholds for the natural regeneration under different management alternatives, as well as the potential impact of climate change [26,27]. Therefore, the objective of the present study was to determine the impact of microclimate conditions (daily rainfall; daily average air and soil temperatures) on the radial expansion of tree stems in the natural regeneration of *Nothofagus antarctica* growing at different forest environments (primary forests, open forests, and edge forests with openlands) in Tierra del Fuego (Argentina). We aimed to answer the following additional questions: (i) what are the dynamics of radial growth during the seasonal cycle in relation to overstory characteristics, and (ii) what is the most important microclimate driver that influences daily growth across the seasons considering different forest environments?

## 2. Materials and Methods

### 2.1. Study Area Characterization

The study was conducted in pure *Nothofagus antarctica* forests located at El Roble ranch (54°06' SL, 67°41' WL) in the central area of Isla Grande of Tierra del Fuego (Argentina). Four transects (1000 m each) were selected, from closed forests to openlands, including three contrasting forest environments: (i) primary forests (CF) with a dominance of mature trees (>150 years old) and closed canopies (>70%); (ii) open forests (OF) with 40–60% overstory cover generated by old thinning (>30 years) for lumber extraction and silvopastoral purposes; and (iii) edge forests with openlands (EF) where regeneration advances over

tussock grasslands (mainly with *Festuca gracillima* and *Empetrum rubrum*) (Figure 1). In these environments, livestock (cows) is the main economic activity, and the animals share their paddocks with natural populations of *Lama guanicoe* (guanaco) [13]. The study area is a long-term permanent plot of the PEBANPA network (Parcelas de Ecología y Biodiversidad de Ambientes Naturales en Patagonia Austral, INTA UNPA CONICET, Argentina) [28].



**Figure 1.** Forest environments studied in the *Nothofagus antarctica*-forested landscapes: CF = closed primary forests, OF = open forests, EF = edge forests with openlands.

For the study area characterization, 12 plots were surveyed (4 transects  $\times$  3 forest environments) in the middle of summer (January to February) by using 50 m transects. Transects were suggested as more convenient sampling methods for these forests in order to capture the stand heterogeneity [3,8–10]. Forest structure was characterized by two subplots located at the beginning and the end of each transect, using the point-sampling method (BAF = 1 to 5) [29] with a Criterion RD-1000 (Laser Technology, Bismarck, ND, USA). At each subplot, we measured the dominant height of the stand using a TruPulse 200 laser clinometer and distance rangefinder (Laser Technology, Bismarck, ND, USA) by averaging the height of the two tallest trees per transect and the diameter at breast height with a forest caliper of each tree. With these data, we obtained the basal area (BA), tree density (TD), and total over-bark volume (TOBV) following models proposed by Ivancich [30]. Overstory canopy cover (OC) and transmitted solar radiation at the understory level (TR) were measured using hemispherical photographs taken in the center of each transect at ground level with an 8 mm fisheye lens (Sigma, Kawasaki-shi, Kanagawa, Japan) mounted on a 35 mm digital camera (Nikon, Japan) with a tripod-leveling head to ensure the horizontal lens position (see details in [3,14]). Additionally, four soil samples were randomly collected along each transect using a field borer with a known volume (230.9 cm<sup>3</sup>) after removing the litter layer. Soil sampling followed a design that was previously successfully implemented in these forests [3,8–10,28]. Soil samples were weighed before and after air-drying in laboratory conditions (24 °C) until reaching a constant weight. Soil bulk density (SD) was obtained from the average of the four samples. After that, coarse root debris of >2 mm and soil aggregations (e.g., small stones and large sand-sized stones) were removed via sieving [3,8]. For chemical analyses, we pooled individual soil samples into one

combined sample per subplot. Each sample was finely ground to below 2 mm using a tungsten–carbide mill, and then, we determined (i) the total organic carbon (SC) from soil samples washed with HCl (50%) using an automatic analyzer (LECO CR12, St. Joseph, MI, USA), (ii) the total nitrogen (SN) using a semi-micro Kjeldahl method, and (iii) the extractable phosphorus (P) according to the method of Bray and Kurtz [31]. Data for nutrient contents are presented as  $\text{kg m}^{-2}$  for the first 30 cm depth using the SD data of each subplot [3,8–10,28]. For animal uses, we followed the modeling proposals of Martínez Pastur et al. [8]. We recorded animal feces from native (*Lama guanicoe*, guanaco) and domestic animals (cows) along each transect ( $50 \times 4 \text{ m}$ ,  $200 \text{ m}^2$ ). We used the number of feces as a proxy of animal use ( $\text{animal ha}^{-1}$ ) by assuming the following: (i) Feces was maintained in the forest floor for a period no longer than a calendar year (decomposition rates are low during summer because of low temperatures and high during winter because of the mechanical effect of snow accumulation) [8,32]. (ii) Average values of defecation per day were defined as 6.0 times per day for guanacos and 12.3 times per day for cows. (iii) The requirements of dry matter forage (palatable plants) varied according to the animals ( $650 \text{ kg DM yr}^{-1}$  for guanacos and  $3250 \text{ kg DM yr}^{-1}$  for cows). In addition, we considered different residual palatable biomass in the understory for further calculations of stocking rate ( $130 \text{ kg DM ha}^{-1}$  for guanacos and  $260 \text{ kg DM ha}^{-1}$  for cows). We sampled the understory following the proposals employed in the PEBANPA network for long-term plots [28]. Finally, (iv) we used sheep equivalents based on the animal species sizes (0.50 for guanaco and 0.16 for cows) to standardize the current livestock density (LD) (for more details, see [8]). To characterize the understory, we used the point-intercept method with 50 intercept points (every 1 m) along each transect [9,28,33]. At each point, we recorded intercepted vascular plant species, bare soil or litter without vegetation (BS), and woody debris cover (DC) ( $>2.5 \text{ cm}$  diameter) to calculate ground cover. With the plant data, we determined understory richness (RIC) and cover (UC). Finally, we collected all live aboveground plant material in a  $0.25 \text{ m}^2$  area associated with each transect and dried it in an oven at  $70 \text{ }^\circ\text{C}$  until we obtained a constant weight, resulting in an estimation of the understory dry biomass (UB) for each subplot [28].

## 2.2. Radial Growth of the Regeneration and Microclimate Characterization

The stem radial growth of the regeneration was monitored using highly precise DEX70 electronic dendrometers ( $\pm 0.05 \text{ mm}$ ) and DEXLOG logger systems (Dynamax, Houston, TX, USA), recording data every 30 min between October and April in two consecutive growing seasons (2018–2019 and 2019–2020). For this, we selected 6 regeneration plants with heights of  $<1.3 \text{ m}$  growing in the representative areas of the studied forest treatments: CF = regeneration starting diameter at measuring points of 0.70 and 0.95 cm; OF = 1.65 and 2.15 cm; and EF = 1.34 and 2.51 cm. Each plant was protected by individual cages (mesh  $2.5 \times 2.5 \text{ cm}$ ) to avoid browsing from guanacos and domestic livestock [2]. At the same place as the dendrometer location, soil water content ( $\pm 0.1\%$ ) was recorded every 30 min with ECHO EC5 soil moisture probes (5 replicas per location) and ECHO Em5b dataloggers (Decagon, Pullman, WA, USA). Additionally, we collected the climatic variables of the study area every 30 min with a portable Davis weather station model, Monitor II (Davis Instruments, Hayward, CA, USA), including rainfall ( $\pm 0.2 \text{ mm}$ ) and air and soil temperatures ( $\pm 0.1 \text{ }^\circ\text{C}$ ). The weather station was located in a nearby open field, uninfluenced by overstory forests ( $\pm 50 \text{ m}$  apart). With the surveyed data, we calculated the daily average values of (i) the diameter growth increment (GI), (ii) the soil water content (SWC), (iii) rainfall, and (iv) temperatures (air and soil). Diameter growth increments were classified into three phases for further analyses: (i) early or lag phase (1 October to 15 November), (ii) medium or exponential phase (15 November to 15 February), and (iii) late or stationary phase (15 February to 30 April) [21,27]. The Southern Oscillation Indexes for each month of the two studied seasons were obtained from the Bureau of Meteorology of the Australian Government ([www.bom.gov.au/climate/enso/soi\\_monthly.txt](http://www.bom.gov.au/climate/enso/soi_monthly.txt) (accessed on 10 April 2023)).

### 2.3. Statistical Analyses

One-way analyses of variance (ANOVA) were conducted using the different forest treatments (CF, OF, EF) as the main factor, comparing forest structure (BA, TD, TOBV, OC), abiotic variables (TR, SD, SC, SN, SP), livestock density (LD), and understory characteristics (RIC, UB, UC, DC, BS). In addition, four multifactorial ANOVAs were performed (i) for the soil water content (SWC) and diameter growth increment (GI) considering forest treatments (CF, OF, EF), growth phases (early, medium, late), and seasons (2018–2019 and 2019–2020) as main factors; (ii) diameter growth increment (GI) considering forest treatments (CF, OF, EF), rainfall (0.0, 0.0–0.2, 0.2–1.0, >1.0 mm day<sup>-1</sup>), and seasons (2018–2019 and 2019–2020) as main factors; (iii) diameter growth increment (GI) considering forest treatments (CF, OF, EF), air temperature (<8.0, 8.0–10.0, >10.0 °C), and seasons (2018–2019 and 2019–2020) as main factors; and (iv) diameter growth increment (GI) considering forest treatments (CF, OF, EF), soil temperature (<8.0, >8.0 °C), and seasons (2018–2019 and 2019–2020) as main factors. Analyses were performed in the Statgraphics Centurion software (StatPoint Inc., Warrenton, VA, USA).

## 3. Results

### 3.1. Changes between the Forest Attributes of the Studied Environments

Significant differences were found in the forest structure (BA, TD, TOBV, OC) where variables were higher in the following order: CF > OF > EF (Table 1). These changes in canopy overstory greatly influenced the microclimate conditions at the understory level (e.g., TR), generating clear gradients (EF > OF > CF), which influences plant biomass (UB). However, understory richness (RIC), cover (UC), and debris cover (DC) were higher in greater overstory covers than in the openlands (CF > OF > EF). Finally, bare soil (BS) was marginally higher in the openlands than under the forest overstory cover. Despite the food offer (i.e., UB) the livestock preferred the open forest canopies (i.e., OF) compared with CF and EF, influencing soil density (SD) and phosphorus content (SP) but not generating significant changes in the other nutrients (e.g., C and N).

The changes in the forest structure and soil properties affected the soil water content (SWC) dynamics (Table 2 and Figure A1). Lower SWC values were found in OF (highly modified soil structure) compared with the other natural environments (CF and EF), and canopy cover (CF > OF > EF) determined the effective rainfall reaching the forest floor. The SWC was greater at the beginning of the growing season (early or lag phase) and then decreased over time (medium or exponential phase and late or stationary phase) when the autumn and winter seasons started to freeze the soil. Finally, significant differences were found in the SWC for the two studied seasons (2018–2019 < 2019–2020), with the first season starting with one La Niña event (SOI = 9.3, December 2018) and experiencing one El Niño event during the late summer (February 2019, SOI = −13.5) and the second season starting with one El Niño event (SOI = −9.3, November 2019). These events determined different rainfall patterns (Tables A1 and A2) that impacted the SWC (Figure A1). Soil water content was higher during the second season for all the forest treatments throughout the monitoring months. Air and soil temperatures were slightly higher during the second season. There were significant climate interactions between the treatments (Figure A1) because the curves of different treatments were correlated several times in both growing seasons.

**Table 1.** One-way ANOVA of forest structure, environmental variables, soil properties, livestock density, and understory biomass and cover considering forest treatments (CF = closed primary forests, OF = open forests, EF = edge forests with openlands) as main factors. BA = basal area ( $\text{m}^2 \text{ha}^{-1}$ ), TD = tree density ( $\text{ind ha}^{-1}$ ), TOBV = total over-bark volume ( $\text{m}^3 \text{ha}^{-1}$ ), OC = overstory cover (%), TR = transmitted radiation at understory level (%), SD = soil bulk density ( $\text{gr cm}^3$ ), SC = soil carbon content ( $\text{kg m}^{-2}$  30 cm depth), SN = soil nitrogen content ( $\text{kg m}^{-2}$  30 cm depth), SP = soil phosphorus content ( $\text{kg m}^{-2}$  30 cm depth), LD = livestock density (sheep equivalent  $\text{ha}^{-1}$ ), RIC = understory richness (n), UB = understory dry biomass ( $\text{kg ha}^{-1}$ ), UC = understory cover (%), DC = debris cover (%), and BS = bare soil (%).

Treatment	BA	TD	TOBV	OC	TR
CF	34.5c	1789b	172.4c	73.1c	37.2a
OF	22.5b	599ab	117.3b	53.7b	61.9b
EF	<0.1a	<1a	<0.1a	7.1a	91.3c
F(p)	42.15 (<0.001)	4.31 (0.048)	44.03 (<0.001)	63.42 (<0.001)	21.41 (0.001)
	SD	SC	SN	SP	LD
CF	0.712a	14.96	0.684	0.422a	1.06a
OF	0.976b	14.31	0.738	0.549b	4.36b
EF	0.802a	13.94	0.691	0.419a	1.02a
F(p)	17.48 (0.001)	0.51 (0.615)	0.47 (0.641)	6.46 (0.018)	4.89 (0.036)
	RIC	UB	UC	DC	BS
CF	37.75b	497.3a	166.5b	6.50b	6.0
OF	36.75b	714.1a	149.0ab	0.50a	7.5
EF	28.25s	3932.8b	116.4a	0.25a	21.5
F(p)	6.53 (0.018)	5.77 (0.024)	6.60 (0.017)	7.61 (0.012)	4.46 (0.045)

F = Fisher test; (p) = probability. Different letters indicate significant differences using a Tukey test at  $p < 0.05$ .

**Table 2.** Multifactorial ANOVA of soil water content (SWC, %) and diameter growth increment (GI,  $\text{mm day}^{-1}$ ) considering forest treatments (CF = closed primary forests, OF = open forests, EF = edge forests with openlands), growth phases during the season (early = before 15 November, medium = 15 November to 15 February, late = after 15 February), and seasons (1 = 2018–2019, 2 = 2019–2020) as main factors.

Treatment	Level	SWC	GI
A: Treatment	CF	26.7b	0.0024
	OP	22.4a	0.0064
	EP	36.9c	0.0134
	F(p)	2296.47 (<0.001)	2.97 (0.052)
B: Phase	Early	30.5c	0.0048a
	Medium	28.5b	0.0176b
	Late	27.1a	−0.0001a
	F(p)	105.5 (<0.001)	11.89 (<0.001)
C: Season	1	25.6a	0.0052
	2	31.8b	0.0097
	F(p)	1190.99 (<0.001)	1.48 (0.224)
Interactions	A × B	22.44 (<0.001)	2.97 (0.019)
	A × C	282.05 (<0.001)	0.03 (0.968)
	B × C	44.29 (<0.001)	0.60 (0.548)

F = Fisher test; (p) = probability. Different letters indicate significant differences using a Tukey test at  $p < 0.05$ .

### 3.2. Daily Growth Increments of Regeneration Growth in Different Forest Environments

The daily growth increment (GI) presented marginal differences ( $F = 2.97$ ,  $p = 0.052$ ) between the forest treatments ( $EF > OF > CF$ ) and showed significant differences throughout

the growing season. Thus, GI increased from the early or lag phase to the medium or exponential phase and decreased to near zero during the late or stationary phase (Table 2 and Figure 1). No significant differences were found between the studied seasons despite the season weather differences described before. Finally, significant interactions between the treatments and phases in the closed forests presented a lower slope in the curves than the other two treatments.

The magnitude of daily rainfall differently influenced the GI based on the forest treatments and phases throughout the seasons (Table 3). In closed forests (CF), daily growth rates were negative, indicating shrinkage in the stems ( $-0.0082$  mm GI day<sup>-1</sup> with no rain and  $-0.0008$  mm GI day<sup>-1</sup> with 0.0–0.2 mm day<sup>-1</sup> of rainfall). Above 0.2 mm day<sup>-1</sup> of rainfall, the GI increased with the amount of daily rainfall. In open forests (OF), daily growth rates were negative only during the days without rain (shrinkage of  $-0.0051$  mm GI day<sup>-1</sup>) and showed a positive GI in relation to the amount of daily rainfall. In edge forests (EF), daily growth rates were always positive, increasing with the amount of daily rainfall. Furthermore, the OF and EF presented significant differences between the phases across the growing seasons, being greater during the medium or exponential phase. Significant interactions were related to the slope curves of the different phases over the growing seasons. The rainfall frequency changed between months (Table A1), e.g., 33% to 66% on days with no rain and 10% to 23% on days with more than 0.2 mm day<sup>-1</sup> of rainfall.

**Table 3.** Multifactorial ANOVA of diameter growth increment (mm day<sup>-1</sup>) for different forest treatments (CF = closed primary forests, OF = open forests, EF = edge forests with openlands) considering growth phases during the season (early = before 15 November, medium = 15 November to 15 February, late = after 15 February), daily rainfall (mm), and seasons (1 = 2018–2019, 2 = 2019–2020) as main factors.

Treatment	Level	CF	OF	EF
A: Phase	Early	0.0154	0.0124ab	0.0133ab
	Medium	0.0058	0.0225b	0.0406ab
	Late	0.0087	0.0087a	0.0091a
	F(p)	0.33 (0.719)	3.01 (0.049)	6.89 (0.001)
B: Rainfall	0.0	$-0.0082^a$	$-0.0051a$	0.0024a
	0.0–0.2	$-0.0008^{ab}$	0.0059a	0.0113a
	0.2–1.0	0.0195 <sup>ab</sup>	0.0161ab	0.0245ab
	>1.0	0.0293 <sup>b</sup>	0.0412b	0.0459b
	F(p)	6.93 (<0.001)	21.03 (<0.001)	7.53 (<0.001)
C: Season	1	0.0065	0.0132	0.0171
	2	0.0134	0.0158	0.0249
	F(p)	0.61 (0.435)	0.23 (0.633)	0.76 (0.385)
Interactions	A × B	1.82 (0.095)	1.25 (0.279)	0.78 (0.586)
	A × C	0.06 (0.944)	0.53 (0.589)	<0.01 (0.997)
	B × C	0.61 (0.612)	3.46 (0.017)	1.02 (0.385)

F = Fisher test; (p) = probability. Different letters indicate significant differences using a Tukey test at  $p < 0.05$ .

The daily average air temperature did not significantly influence GI and phases based on the forest treatments (Table 4); however, higher values were found at 8.0–10.0 °C for all treatments. Despite this, only phases across the seasons presented significant differences, as has been described before. Finally, the daily average soil temperature showed significant differences only for EF, being greater for temperatures above 8.0 °C (Table 5). The frequency of occurrence of each temperature category changed between different months (Table A1), e.g., most air and soil temperatures in October and April were <8.0 °C, while in summer (December to February), they were >8.0 °C.

**Table 4.** Multifactorial ANOVA of diameter growth increment ( $\text{mm day}^{-1}$ ) for different forest treatments (CF = closed primary forests, OF = open forests, EF = edge forests with openlands) considering growth phases during the season (early = before 15 November, medium = 15 November to 15 February, late = after 15 February), daily average air temperature ( $^{\circ}\text{C}$ ), and seasons (1 = 2018–2019, 2 = 2019–2020) as main factors.

Treatment	Level	CF	OF	EF
A: Phase	Early	0.0028	−0.0011a	0.0001ab
	Medium	−0.0011	0.0159b	0.0271b
	Late	−0.0013	0.0002ab	−0.0003a
	F(p)	0.07 (0.934)	4.64 (0.010)	6.47 (0.002)
B: Air temperature	<8.0	−0.0039	0.0044	0.0091
	8.0–10.0	0.0015	0.0086	0.0104
	>10.0	0.0028	0.0021	0.0072
	F(p)	0.24 (0.787)	0.34 (0.709)	0.03 (0.966)
C: Season	1	−0.0005	0.0035	0.0058
	2	0.0007	0.0066	0.0121
	F(p)	0.02 (0.888)	0.37 (0.543)	0.67 (0.413)
Interactions	A × B	0.66 (0.618)	0.35 (0.846)	0.86 (0.490)
	A × C	0.53 (0.590)	0.34 (0.713)	0.72 (0.488)
	B × C	0.41 (0.662)	0.13 (0.874)	0.52 (0.594)

F = Fisher test; (p) = probability. Different letters indicate significant differences using a Tukey test at  $p < 0.05$ .

**Table 5.** Multifactorial ANOVA of diameter growth increment ( $\text{mm day}^{-1}$ ) for different forest treatments (CF = closed primary forests, OF = open forests, EF = edge forests with openlands) considering growth phases during the season (early = before 15 November, medium = 15 November to 15 February, late = after 15 February), daily average soil temperature ( $^{\circ}\text{C}$ ), and seasons (1 = 2018–2019, 2 = 2019–2020) as main factors.

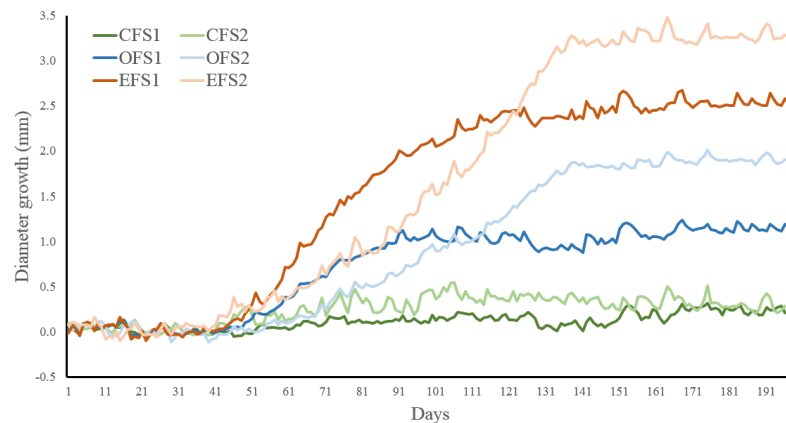
Treatment	Level	CF	OF	EF
A: Phase	Early	−0.0007	0.0029	0.0074
	Medium	0.0109	0.0012	−0.0158
	Late	−0.0043	−0.0019	−0.0039
	F(p)	0.21 (0.809)	0.12 (0.180)	0.64 (0.527)
B: Soil Temperature	<8.0	0.0062	−0.0073	−0.0234a
	>8.0	−0.0022	0.0088	0.0152b
	F(p)	0.24 (0.626)	1.8 (0.180)	4.87 (0.028)
C: Season	1	0.0011	0.0001	−0.0056
	2	0.0028	0.0013	−0.0026
	F(p)	0.02 (0.894)	0.04 (0.849)	0.10 (0.748)
Interactions	A × B	0.49 (0.615)	0.28 (0.754)	1.58 (0.207)
	A × C	0.96 (0.328)	0.16 (0.689)	0.06 (0.799)
	B × C	0.85 (0.428)	0.16 (0.852)	0.11 (0.899)

F = Fisher test; (p) = probability. Different letters indicate significant differences using a Tukey test at  $p < 0.05$ .

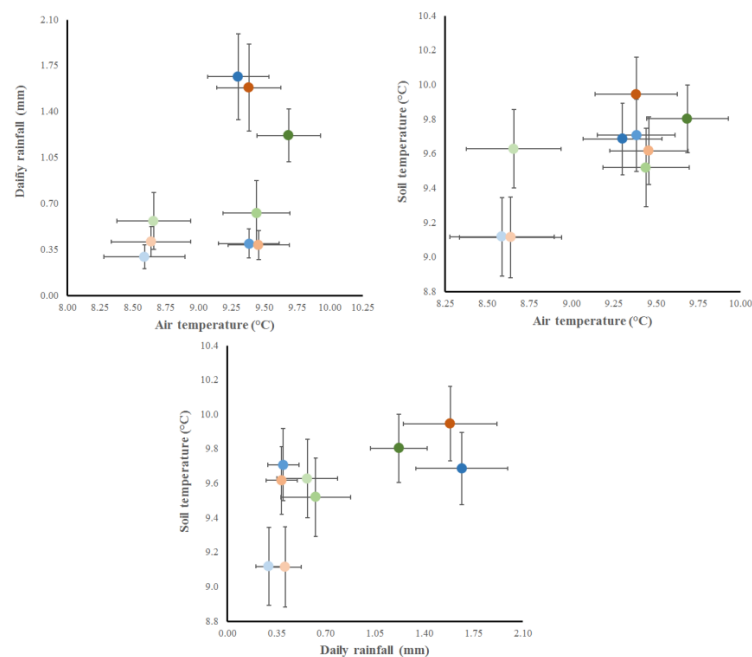
The interactions between climate variables (daily rainfall; air and soil temperatures) affected the diameter growth increment of the regeneration of the different forest environments (Figure 2). However, it was clear that the magnitude of the climate variables influenced more than the forest environment itself. When the daily rainfall was correlated with air temperatures, higher GI values were positively correlated with higher amounts of rainfall and air temperatures. Furthermore, medium values of the GI were found with



lower amounts of daily rainfall and higher air temperatures. The lowest GI values were found with lower daily rainfall and air temperatures. In this sense, higher rainfall values only influenced GI values when the air temperatures were higher than 9 °C. When daily rainfall was correlated with soil temperatures, higher GI values were also positively correlated (e.g., higher amounts of rainfall and soil temperatures) (Figure 3). Low and medium GI values were found with lower amounts of daily rainfall, and high rainfall values only influenced GI values when the soil temperatures were higher than 9.4 °C and rainfall was higher than 1.0 mm day<sup>-1</sup>. The third comparison analyzed the relationship between air and soil temperatures, where the medium and higher GI values occurred at higher values of both variables. However, at the lower GI values, the influence of soil temperatures was higher on openlands (EF) than on different forest canopies (CF-OF).



**Figure 2.** Diameter growth during the growing season (mm) (S1 = 2018–2019 in dark colors, S2 = 2019–2020 in pale colors) for the different forest treatments (CF = closed primary forests in green, OF = open forests in blue, EF = edge forests with openlands in orange). Days start at the beginning of October for each season.



**Figure 3.** Diameter growth increment relationships across the season (pale, medium, and dark colors represent low-to-high values) between daily rainfall (mm), daily average air (°C), and soil temperature (°C) for the different forest treatments (CF = closed primary forests in green, OF = open forests in blue, EF = edge forests with openlands in orange). Bars represent the standard error of the axis values for each treatment.

Another consideration was the growth pattern throughout the season for the different studied treatments (Figure 2). These patterns changed in magnitude between seasons but maintained their behavior under the different treatments: (i) closed primary forests did not greatly change throughout the season, (ii) open forests presented an expected sigmoid growth curve, and (iii) edge forests with openlands presented a straight growth that linearly increased from the start of the growth period and then abruptly ended.

## 4. Discussion

### 4.1. The Influence of Overstory Cover and Management Practices on Forest Attributes

Natural forests of *N. antarctica* follow simple gap dynamics, and the decay of mature trees or the local windthrow promotes the development of regeneration based on seed and agamic reproduction (e.g., root sprouts) [3,34]. The recruitment and survival of seedlings are mainly related to the balance between light and soil moisture availability, as well as other abiotic factors such as animal browsing (livestock and natural populations of *Lama guanicoe*) [8,13,33] and understory cover [9–11]. In mature or secondary forests without management (CF), the overstory decreases the light availability, affecting the understory biomass and biodiversity values in relation to the age structure of the trees [8].

Silvopastoral systems (OF) are proposed to manage these forests, with thinning increasing the understory biomass to maximize livestock production [2], but this may generate a decrease in species richness [6,35]. Animal use at a high stocking rate modifies some soil layer characteristics, e.g., it increases soil density and phosphorus and nitrogen contents because of manure deposits [8,36,37]. The ecotone environments between forests and grasslands (EF) present greater understory biomasses with lower plant richness and more bare soil because of greater wind exposure [38,39]. The described changes influence livestock density, as animals prefer managed forests (OF) compared with closed forests (CF) because of better pastoral allowance and compared with open environments (EF) for better environmental conditions [8]. Furthermore, the stand microclimate and soil conditions change because of management and condition regeneration recruitment, growth, and survival [40,41].

### 4.2. Regeneration Growth in Different Forest Environments

The soil water content greatly varied within the growing season and between years, which shows that it is a limiting factor in natural regeneration and can greatly influence annual growth. Contrary to our expectations, we found less soil water content in the managed forests (OP < CF < EP), probably because of higher soil density in the upper soil layer caused by compaction [3,8]. At these high latitudes, the soil water content decreases from late spring to late summer, mainly related to the melted snow accumulated during the winter season, which can influence the entire growing season (e.g., higher snow accumulation during winter promotes higher water availability in soil during summer) [42]. As was expected, the mean diameter growth of the regeneration (mm day<sup>-1</sup>) decreased with the overstory canopy, as has been cited for other *Nothofagus* species [43], and followed the expected response across the different growth development phases over the season [44], but it did not significantly change between years despite the described differences. However, the trend showed higher growth during the humid years compared to the drier ones. The soil moisture trend across the seasons and years (Figure A1) can be related to the regeneration growth rates (Figure 2). The first year presented a drought period during the late summer, which promoted the end of growth before the performance observed during the second year, which was more humid. Most of the research on growth (height, diameter, biomass) considered the full season and relates these values to average climate values of the year or specific months (e.g., summer) [11,19,43]. However, the yearly growth performance can be influenced for small critical periods of time and not necessarily for all the months during the growing season. Drought effects have been previously described for many *Nothofagus* species and reveal the structure of future forests under climate change with more frequent drought events [45–47].

Daily stem dynamic studies have been reported as a useful tool by several studies [48,49], with dendrometers being a useful tool for the long-term, high-resolution monitoring of tree responses to environmental fluctuations and climate change [50]. In our study, the response of the regeneration radial growth to the microclimate and resource availability was heterogeneous between the different forest environments, evidencing different levels of resilience in the regeneration growth under these different conditions in the face of changes in the forest structure [15,51]. Unmanaged forests (CF) did not significantly change the regeneration growth rates over the season compared with open environments (OF and EF), which followed the expected growth rates (e.g., the early, exponential, and stationary phases). These growth rates are directly related to daily rainfall, and the amount of water that reaches the forest floor is proportional to the canopy overstory cover [14,38,40]. The unmanaged forests (CF) had lower resilience than the managed stands (OF) and edge forests (EF), where negative growth (shrinking diameters) was observed ( $<0.2 \text{ mm day}^{-1}$  in CF and days without rainfall in OF). Negative growth is associated with root mortality and tree decay, as previously reported for other *Nothofagus* species at these latitudes [21]. The outputs suggest that regeneration growth in unmanaged forests is more vulnerable to drought periods than in more open areas. The higher mortality rates in the higher overstory canopies have been previously described [2,30,51], but this is the first time that the growth rates of regeneration were linked to daily rainfall events.

The measured radial growth rates of the regeneration were not related to air temperatures. However, some trends can be observed; e.g., lower growth rates occurred at lower and higher temperatures (maximum growth rates found in open areas were observed at daily temperatures between 8 and 10 °C). This is the main reason for the start of regeneration growth at the beginning of the season after day 50 [30,40].

A similar trend was observed for soil temperatures; however, significant differences were found in the edge forests (EF), where positive values were obtained in soil temperatures  $>8 \text{ °C}$ . The temperature (air and soil) can be a limiting factor in some forest ecosystems [52,53], where soil temperatures determine the activity periods of roots and, as a consequence, entire plants [54]. Soil temperature has complex effects on trees and soil, which can affect carbon dynamics in forest ecosystems [55]. There were positive and negative synergies when the microclimate factors were analyzed together (Figure 3). The higher growth rate values for the three studied environments were found with high daily rainfall and temperatures (both air and soil). From this, the threshold was determined for a daily rainfall value of  $1 \text{ mm day}^{-1}$  or an air temperature of 9 °C. Growth dynamics were not solely driven by soil temperature, but resource competition also played a significant role [55], which can be influenced by other microclimate factors. These synergies in growth were reported by Dantas et al. [56], who determined that rainfall, not soil temperature, limits seed germination in dry forest species. Similarly, Belyazid et al. [57] showed that reduced soil water availability in summer seasons will strongly limit the expected gain in weathering associated with higher temperatures. These positive and negative synergies are directly related to the overstory, which influences biotic and abiotic conditions; e.g., microclimates within a regenerating forest change with increasing distance from a mature forest edge, which determines the magnitude of microclimatic change variations over diurnal, seasonal, and successional time scales [44]. Climatic events such as the ENSO phenomenon greatly influence forest dynamics at the regional level [58] and could lead to positive and negative synergies in natural and managed forests [59,60].

Regeneration growth is expected following a typical sigmoid growth curve, which has been described before for different *Nothofagus* species [14,21,25]. However, in our study, we found two different growth patterns for OF and EF. The first one followed the sigmoid growth curve, while the second presented a straight growth that linearly increased at the start of the season and then abruptly ended. Our study did not clearly identify this change in the growth pattern; it is interesting future research that will remain unsolved for now and is probably related to abrupt changes in the microclimate in the openlands. Other studies have also identified non-uniform growth dynamics in changed climate conditions [22,50].

### 4.3. Management Implications

Climate change defines new levels of global rainfall and mean temperatures and the recurrence of extreme events (e.g., the length of growing periods) [61,62]. The resilience capacity of *Nothofagus* forests in recovering canopy cover losses is based on seedling banks and seedling survival [63–65]. However, seedling banks can survive for long periods of time waiting for the canopy to open, and the resilience capacity is based on their regeneration survival capacity [11,12]. For this, consecutive drought periods over the season can lead to decreases in the growth rate and consequently raise seedling death rates. Other studies related to the impact of climate change on forest regeneration confirm negative and positive synergies, highlighting the importance of site-specific effects [38,65–67].

Silvopastoral systems in *N. antarctica* forests have been designed to improve the timber quality of trees and, at the same time, increase the forage availability for livestock [2,28]. One of the main challenges is assuring tree strata continuity based on tree regeneration. For this, natural regeneration must be enhanced and protected from limiting factors (e.g., overbrowsing) until trees can freely develop in managed stands [2]. This study showed that canopy opening improves the radial growth rates of natural regeneration and improves resilience in the face of long drought periods compared with unmanaged stands. These findings provide thresholds for regeneration survival, allowing us to develop more sustainable silvicultural practices [67]. We suggest following a strategy of adaptive management [68] based on the long-term monitoring of local extreme climate events, e.g., the PEBANPA network [28]. In this sense, this study highlights the need for more sustainable management strategies to maintain ecosystem functions and resilience by reducing forest degradation in the face of potential climate change impacts.

## 5. Conclusions

Forest dynamics and harvesting modify stand conditions, influencing the microclimate and natural cycles. The resilience of radial regeneration growth in the face of these changes is modified according to the overstory forest structure, including the direct relationships between the availability of light, temperature, and soil moisture. The temperature (air and soil) and daily rainfall events influence daily regeneration growth, leading to increases or decreases in diameter based on the magnitude of such events. The outputs indicate that the regeneration of *Nothofagus antarctica* is vulnerable to non-rainy days in relation to the crown cover of the stands, changing the vulnerability across the growing season. Furthermore, the magnitude of these changes is also related to the year, e.g., the presence of drought periods during the summer. Another unexpected finding showed non-uniform growth dynamics in the different studied environments, highlighting the chance of the existence of different thresholds and microclimate conditions for the different studied environments. The main findings of this research identify different thresholds for natural regeneration growth, which can influence recruitment and survival, leading to limitations on current management proposals. These outputs suggest the need for new studies and long-term monitoring to develop more robust silvicultural proposals to face climate change and more frequent extreme events because the forest term at these latitudes exceeds hundreds of years.

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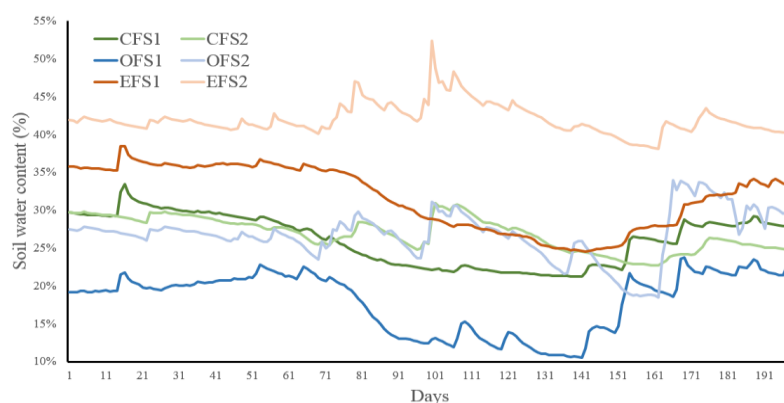
**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** The data and materials are available at the CADIC-CONICET (Argentina) repository.

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## Appendix A



**Figure A1.** Soil water content (%) during the growing season (S1 = 2018–2019 in dark colors, S2 = 2019–2020 in pale colors) for the different forest treatments (CF = closed primary forests in green, OF = open forests in blue, EF = edge forests with openlands in orange). Days start at the beginning of October for each season.

**Table A1.** Weather station values by month (October to April) during both growing seasons (2018–2019, 2019–2020) for rainfall (RAIN, mm month<sup>-1</sup>), average air temperature (°C), and average soil temperature (°C).

Season	Month	Rain	AT	ST
2018–2019	OCT	32.8	5.2	4.6
	NOV	16.4	8.5	8.2
	DEC	27.6	10.7	10.6
	JAN	20.4	9.9	10.8
	FEB	20.2	9.4	10.7
	MAR	33.8	8.5	9.1
	APR	40.4	4.8	5.8
2019–2020	OCT	12.6	5.5	5.3
	NOV	31.0	7.7	7.9
	DEC	45.6	10.3	10.5
	JAN	52.0	10.8	11.4
	FEB	14.0	10.8	11.7
	MAR	20.8	8.4	9.5
	APR	3.1	4.6	5.5

**Table A2.** Frequency of days by month and full season (October to April) during both growing seasons (2018–2019, 2019–2020) according to the studied levels of daily rainfall (mm), daily average air temperature (°C), and daily average soil temperature (°C).

Rainfall	0.0	0.0–0.2	0.2–1.0	>1.0
OCT	64.5%	16.1%	9.7%	9.7%
NOV	60.0%	10.0%	11.7%	18.3%
DEC	66.1%	9.7%	12.9%	11.3%
JAN	50.0%	16.1%	14.5%	19.4%
FEB	51.3%	25.6%	12.8%	10.3%
MAR	51.6%	12.9%	12.9%	22.6%
APR	33.3%	33.3%	13.3%	20.0%
SEASON	56.1%	16.2%	12.4%	15.3%
Air temperature	< 8.0	8.0–10.0	> 10.0	
OCT	88.7%	4.8%	6.5%	
NOV	46.7%	33.3%	20.0%	
DEC	12.9%	19.4%	67.7%	
JAN	12.9%	32.3%	54.8%	
FEB	33.3%	17.9%	48.7%	
MAR	41.9%	25.8%	32.3%	
APR	90.0%	10.0%	0.0%	
SEASON	43.9%	21.1%	35.0%	
Soil temperature	< 8.0	> 8.0		
OCT	100.0%	0.0%		
NOV	40.0%	60.0%		
DEC	0.0%	100.0%		
JAN	0.0%	100.0%		
FEB	0.0%	100.0%		
MAR	6.5%	93.5%		
APR	86.7%	13.3%		
SEASON	32.9%	67.1%		

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