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UNIVERSIDAD DE CHILE - FACULTAD DE CIENCIAS - ESCUELA DE  
PREGRADO

**SEED PRODUCTION AND PRE-DISPERSAL SEED PREDATION OF  
*Nothofagus glauca* AND *Nothofagus obliqua* IN THE FRAGMENTED MAULINO  
FOREST OF CHILE**

**PRODUCCIÓN Y DEPREDACIÓN PRE-DISPERSIÓN DE SEMILLAS DE  
*Nothofagus glauca* Y *Nothofagus obliqua* EN EL FRAGMENTADO  
BOSQUE MAULINO DE CHILE**

Seminario de Título entregado a la Universidad de Chile en cumplimiento parcial de los requisitos para optar al Título de Bióloga con mención en Medio Ambiente.

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Junio, 2010  
Santiago - Chile



## INFORME DE APROBACIÓN SEMINARIO DE TÍTULO

Se informa a la Escuela de Pregrado de la Facultad de Ciencias, de la Universidad de Chile que el Seminario de Título, presentado por la Srta. Gianina Mackarena Romero Vásquez

### “SEED PRODUCTION AND PRE-DISPERSAL SEED PREDATION OF *Nothofagus glauca* and *Nothofagus obliqua* IN THE FRAGMENTED MAULINO FOREST OF CHILE”

Ha sido aprobado por la Comisión de Evaluación, en cumplimiento parcial de los requisitos para optar al Título de Bióloga con mención en Medio Ambiente.

*Dr. Javier A. Simonetti*  
Director Seminario de Título

#### Comisión de Evaluación

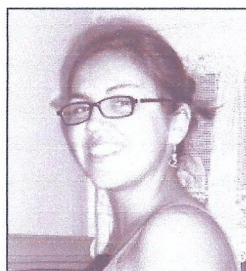
*Dr. Ramiro Bustamante*  
Presidente Comisión

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Santiago de Chile, 22 Julio 2010

## Biografía



Segunda hija de Francisco Romero y Jeannette Vásquez, hermana de Enrique y Katherine, nací un 1° de junio de 1987 en Santiago, Chile. A los dos meses de vida junto a mi familia emprendí viaje con destino a Bergen, Noruega, ciudad donde pasaría los primeros 5 años de mi vida y aprendería una particular visión del mundo. Durante mi desarrollo educacional, estudié en un gran número de colegios, comenzando mis primeros años de estudios en la Escuela Aldea María Reina, continuando en Nygård Sskole en Bergen, pasando luego por el Complejo Educacional Fernando de Aragón y la Escuela Los Andes, para culminar mi educación media en el Colegio Estela Segura. Durante los últimos años de educación media, caería en cuenta que quería seguir el rumbo de las ciencias. Es así como en el año 2005 con 17 años de edad ingresé a Biología con mención en Medio Ambiente, en la Universidad de Chile. Luego de intensos años dentro y fuera de las aulas de la facultad, y tras un fugaz paso con la botánica, conocería la Biología de la Conservación de mano del Dr. Javier Simonetti. Entre los años 2008-2009, realicé mi práctica profesional en Wildlife Conservation Society Chile, dentro del marco de la conservación de ecosistemas de turberas. Durante el 2009 y principios de 2010 realizaría mi seminario de título con el Dr. Javier Simonetti, abordando los efectos de la fragmentación de bosques sobre la producción y depredación pre-dispersión de semillas de *Nothofagus glauca* y *N. obliqua* en el bosque Maulino costero.

*A mis padres, hermanos  
y compañero de rumbo*





## Agradecimientos

Agradezco a todos los que participaron en esta investigación y ayudaron en alguna medida a la elaboración de este seminario de título. A mi tutor Dr. Javier A. Simonetti por su dedicación y paciencia. A mis padres, hermanos, y compañero de rumbo por su apoyo incondicional durante el largo proceso. A Ronny Zúñiga por su vital ayuda y paciencia en el laboratorio. A mis compañeros Renzo Vargas, Francisco Fontúrbel, Robert Márquez y Paula Giraldo por su ayuda en terreno y orientaciones en el laboratorio. CONAF VII Región por autorizar los trabajos en la Reserva Nacional Los Queules y a Forestal Masisa S.A. por permitir trabajar en sus terrenos en Tregualemu. A la Dirección Meteorológica de Chile por facilitar información de la estación meteorológica de Chanco. El estudio fue financiado por FONDECYT 1010852 y 1050745.

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## Resumen

La fragmentación de bosques es una amenaza global para la biodiversidad, alterando su composición, estructura y funciones en fragmentos remanentes. Hasta la fecha, pocos estudios han tratado los efectos de la fragmentación sobre la producción de semillas. La producción de semillas se correlaciona con factores climáticos, como temperatura y precipitación, durante periodos claves que preceden a la lluvia de semillas. En este estudio, esperamos un aumento de la producción de semillas de *Nothofagus glauca* y *N. obliqua* en fragmentos respecto al bosque continuo, debido a que los fragmentos serían más cálidos y secos; además esperamos una depredación de semillas pre-dispersión similar entre ambos hábitats; y si la saciación de depredadores ocurre, entonces esperamos encontrar una mayor proporción de semillas libres de depredación pre-dispersión durante años de alta producción de semilla. El objetivo de este seminario de título es comparar la producción de semillas y depredación de semillas pre-dispersión de *N. glauca* y *N. obliqua* entre fragmentos y un área continua de bosque Maulino en la costa Mediterránea de Chile central durante una serie de tiempo de 7 años, para determinar un efecto de la fragmentación sobre ellos. La depredación de semillas pre-dispersión fue evaluada en semillas producidas en las siete temporadas consecutivas (2002-2009) en el bosque continuo y fragmentos. La producción de semillas del bosque continuo se encuentra correlacionada con la de los fragmentos en ambas especies. Entre los años 2003-2008, la producción de semillas promedio de *N. glauca* fue 84.5 veces mayor en el bosque continuo que en los fragmentos, mientras que la de *N. obliqua* fue 14.7 veces mayor en fragmentos que en bosque continuo. La producción de semillas de *N. glauca* fue significativamente menor en fragmentos de bosque, mientras que la de *N. obliqua* fue significativamente mayor en fragmentos. Los máximos de producción de semilla anual en *N. glauca* suceden entre 2 a 4 años, mientras que en *N. obliqua* suceden cada 2 años. La depredación de semillas pre-dispersión afectó un 43.1% de semillas de *N. glauca* del bosque continuo y a un 8.3% de las de los fragmentos, y a un 14.9% de semillas de *N. obliqua* en ambos hábitats. La producción de

semillas de *N. obliqua* en ambos hábitats y de *N. glauca* en bosque continuo no se correlacionó con la precipitación y temperaturas medias, mínimas y máximas durante el desarrollo de primordios florales y la floración. La producción de semillas de *N. glauca* en fragmentos se correlaciona negativamente con las temperaturas medias, mínimas y máximas durante el desarrollo de los primordios florales y temperatura máxima durante la floración. La depredación pre-dispersión de semillas es independiente de la producción de semillas en ambas especies. Nuestros resultados en conjunto con estudios previos, sugieren que la composición, estructura y funciones del bosque Maulino pueden ser afectadas por la fragmentación, mediante diferencias significativas en la producción de semillas de *N. glauca* y *N. obliqua* de fragmentos y bosque continuo, la cual es deprimida o aumentada respectivamente, en fragmentos de bosque Maulino.

**Palabras clave:** Fragmentación de bosque, *Nothofagus glauca*, *Nothofagus obliqua*, producción de semillas, depredación pre-dispersión de semillas.

## Abstract

Forest fragmentation is a global threat to biodiversity, altering the composition, structure, and functions in remnant fragments. At the date, few studies treated fragmentation effects on seed production. Seed production was correlated with climate factors (i.e. temperature and precipitation) during key periods preceding seed rain. We expected an increase in seed production of *Nothofagus glauca* and *N. obliqua* in fragments regard to continuous forest, due to fragments were more warm and drier; we further that pre-dispersal seed predation be similar among habitats; and if predator satiation occurs, found a higher proportion of seeds free of pre-dispersal predation during years of higher seed production. Thus, the objective of this study was to compare seed production and pre-dispersal seed predation of *N. glauca* and *N. obliqua* among fragments and continuous area of the Maulino forest in the Mediterranean coast of central Chile during a 7 years series time, to determine if there was a fragmentation effect on them. Pre-dispersal seed predation was evaluated in seeds produced throughout seven consecutive seasons (2002-2009) in continuous forest and forest remnants. Seed production was correlated among continuous forest and fragments for both species. During 2003-2008, the average of annual seed production of *N. glauca* seed production was 84.5 times higher in continuous forest than forest fragments, whilst *N. obliqua* seed production is 14.7 times higher in fragments than in continuous forests. During all seasons, *N. glauca* seed production was significantly lower in small fragments, while *N. obliqua* seed production was significantly higher in fragments. Maximum annual production of *N. glauca* occurs every 2 to 4 years, while in *N. obliqua* occurs every 2 years. Pre-dispersal seed predation occurred in the 43.1% of *N. glauca* seeds from continuous forest and 8.3% from fragments, while occurred in 14.9% of *N. obliqua* seeds from each habitat. There was no correlation among seed production of *N. obliqua* from both habitats and *N. glauca* of continuous forest with precipitation, average, minimum or maximum temperatures during floral primordia development and flowering. *N. glauca* seed production of fragments was negatively correlated whit average, minimum and maximum temperatures during floral

primordial development and maximum temperatures during flowering. Pre-dispersal seed predations were not correlated with seed production for either species. Our results along with previous studies, suggest that Maulino forest composition, structure and functions might be affected by forest fragmentation, throughout significantly differences in seed production of *N. glauca* and *N. obliqua* among continuous forest and fragments, which been depressed and increased respectively in fragments of Maulino forest.

**Key words:** Forest fragmentation, *Nothofagus glauca*, *Nothofagus obliqua*, seed production, pre-dispersal seed predation.

## 1. Introduction

Forest fragmentation is a global threat to biodiversity, altering the composition, structure, and functions of biodiversity in remnant fragments (Chapin et al., 2000; Fahrig, 2003). These changes in ecological interactions and processes can eventually affect the dynamics of vegetation at remnant fragments (Laurance, 2002). Seed production for instance might be affected by microclimate changes such as an increased light and air temperature, decreased soil and air moisture and greater temperature fluctuations and wind disturbances compared with the forest continuous (Kapos 1989, Murcia 1995, Didham and Lawton, 1999), variables that impinge upon seed production (Richardson et al., 2005). Microclimate changes can also affect directly germination and seedling establishment (Bruna, 1999, 2002).

Recruitment can also be indirectly affected by pre and post-dispersal seed predation (Janzen, 1970; Harper, 1977; Schelin et al., 2004; Vallejo-Marín et al., 2006; Diaz-Fleischer, 2010). Habitat fragmentation can decrease pre-dispersal seed predation probably due to a reduction in the abundance, diversity and species richness of seed predators (Didham et al., 1996, Chacoff et al., 2004), increasing the number of seeds available for germination in fragments.

Despite the potential impact of fragmentation on seed production, the available information related to seed production in fragmented forests is scarce. A review of studies regarding seed production in fragmented environments (using the *ISI Web of Knowledge* searcher between years 1998-2008, using the keywords "forest\* fragment\*" and "seed production") reveals that from a total of 3254 papers related to forest fragmentation, only 42 articles (1.8% of total) refers to seed production, and it five (0.15% of total) compare forest fragments and continuous forest.

Seeds and flowers production could be modified by higher temperatures and lower humidity during floral induction, as could be faced in fragments, in a variety of taxa (Piovesan & Adams; 2001; Schauber et al., 2002; Kon et al., 2005; Richardson et al., 2005). For instance, seed production in anemophilous species such as *Fagus crenata* is negatively correlated with the spring temperature of the year preceding flowering (Kon et al., 2005), while in another anemophilous species such as *Nothofagus solandri*, high seed production is associated with warm summers at the development of floral primordia (Richardson et al., 2005). Therefore, microclimate changes in forest fragments could modify seed production. Otherwise, seed production in forest fragments can be depressed by reduction of pollinators abundance and pollen limitation (Cunningham, 2000; Ward and Johnson, 2005, O'Connell et al., 2006, Valdivia et al., 2006), due to changes in the quantity and quality of pollen in fragments (Knight, 2003).

Seed production varies across years. Masting, the synchronous production of large seed crops by population of plants (Janzen 1969, 1971, Silvertown 1980, Kelly and Sork 2002) is expected to increase the likelihood of recruitment because swamping the environment with seeds would benefit plant populations through satiate seed predators, allowing a higher proportion of seeds to survive and germinate (Janzen 1971, Jensen 1982, McKone et al. 1998). Up to date, despite an increasing number of studies dealing with seed predation in fragmented forests (i.e. Donoso et al., 2003; Chacoff et al., 2004; Burgos et al., 2008), no studies has yet focused on whether fragmentation affects pre-dispersal seed predation during masting episodes. Due to microclimatic changes in the fragments it could result in an increase of seed production, it would be interesting to determine if fragmentation affects pre-dispersal seed predation during masting episodes, which could result into an increment of recruitment in fragments.

The Maulino forest of central Chile is a highly fragmented environment, where vegetation dynamic of fragments differs from continuous forest (Bustamante et al., 2005; Ramos et al., 2008). *Nothofagus obliqua* and *Nothofagus glauca* two dominant species are anemophilous so fluctuations in seed production could not be associated with a reduction in the abundance of pollinators. Furthermore, *N. glauca* and *N. obliqua* density are 6.1 and 52.7 times higher in fragments than in continuous forest, respectively (Lagos, 2007). Therefore fluctuations in seed production in fragments could not either be associated with pollen limitation in fragments.

*Nothofagus glauca* and *N. obliqua* present a multi-annual pattern of seed production, with maximum production occurring approximately every 5 and 3 years, respectively (Donoso, 1982; Murúa and Gonzalez, 1985). Like in other *Nothofagus* species, seed production is related to climatic conditions during flowering period. High production is associated with high temperatures and low rainfall (Murúa and Gonzalez, 1985; Burgos et al., 2008). Seed production of *N. glauca* varied both in space and time. In a fragmented coastal Maulino forest, seed production was significantly higher in continuous forest compared to forest fragments during 2006, difference explained by microclimatic conditions (Burgos et al., 2008), such as differences in soil humidity and air temperature between continuous forest and fragments (Henríquez, 2002; Rubio & Simonetti, 2009). Pre-dispersal seed predation of *N. glauca* on the other hand did not show significant differences between continuous forest and fragments (Burgos et al., 2008), contrasting with findings in other fragmented environments, where pre-dispersal seed predation is lower in forest fragments (e.g. Chacoff et al., 2004). Attending that only two years of seed production and pre-dispersal seed predation have been studied, and only for *N. glauca*, in this work we compare such variables in a fragmented coastal Maulino forest for a longer period of time, embracing potential differences in seed production through the years. In this framework, we expected an increase in seed production of *N. glauca* and *N. obliqua* in forest fragments regarding a continuous forest, because fragments are warmer and drier than the continuous forest; we further

hypothesized that pre-dispersal seed predation will be similar in the continuous forest and forest fragments, based on the 2-year study for *N. glauca* in the Maulino forest (Burgos et al., 2008); finally if predator satiation occurs, a higher proportion of seeds will be free of pre-dispersal predation during years of higher seed production.



## 2. Methods

### 2.1 Study area

The Maulino forest is an endemic temperate forest located along the coast between 35° 55'S and 37°20'S. Dominant species are *Nothofagus glauca* and *Nothofagus obliqua*, which coexist with many endemic species such as *Gomortega keule* (Gomortegaceae), *Pitavia punctata* (Rutaceae), *Nothofagus pumilio* and *Nothofagus alessandri* (Nothofagaceae), some of them of conservation concern (San Martín and Donoso, 1996). Since the late nineteenth century, the Maulino forest has been fragmented due to their replacement by commercial plantations of *Pinus radiata* and other species employed in agriculture (Bustamante et al., 2005).

### 2.2 Study species

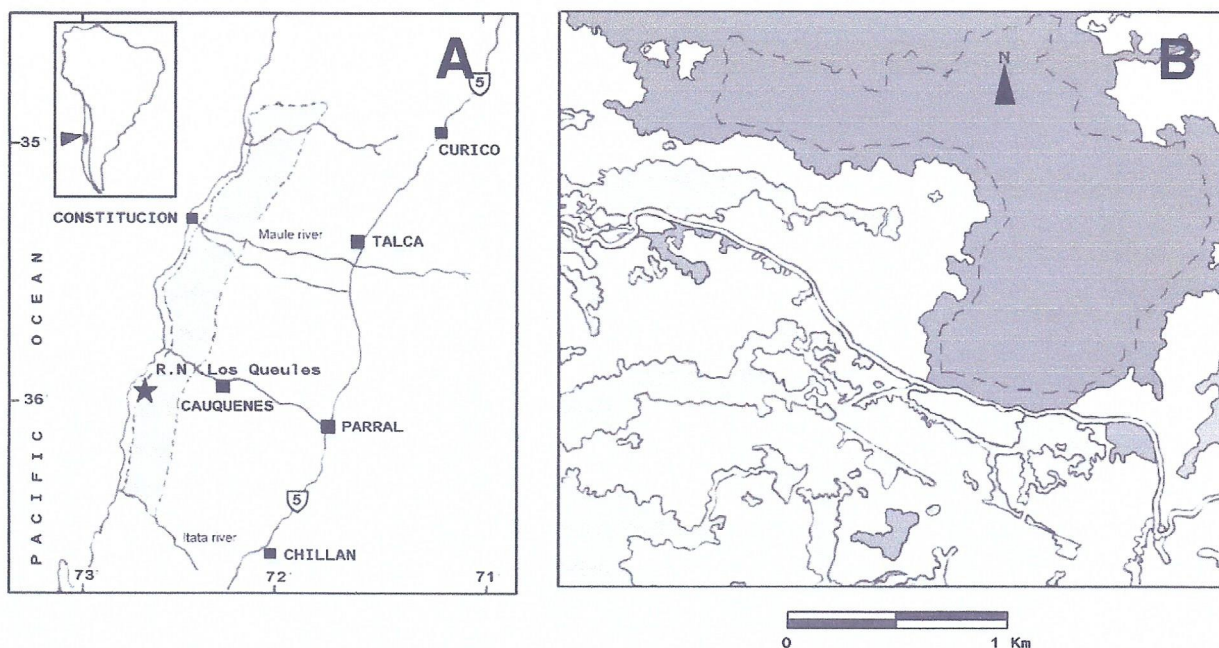
*Nothofagus glauca* and *N. obliqua* are two deciduous, broad-leaved species. In *Nothofagus* genus, initiation of flower buds occurs during the autumn, three months later the male flowers emerge followed by female flowers a week later (Donoso, 1994). Their fruits contain three nuts and ripen between November to April, when seed rain occurs (Donoso and Ramírez, 1994; Burgos et al., 2008). Both species has pre-dispersal seed predators, as the larvae of the microlepidopteran *Perzelia* sp in the case of *N. glauca* (Cruz, 1981; Burgos et al., 2008) and a non-identified microlepidopteran larva in *N. obliqua*. *Perzelia* sp has an annual life cycle, and its larvae emerge from August to November, similar to the flowering of *N. glauca* (Morales, 1993; Rojas, 1996). In *N. glauca*, the very hard coat seed makes improbable the oviposition of *Perzelia* sp after dispersion. This is supported by the absence of adults flying around infested seeds after dispersion (Cruz, 1981; Burgos et al., 2008).

### 2.3 Sampling design

Seed samples were collected in a continuous forest and four small forest fragments. Continuous forest corresponds to the protected area "Reserva Nacional Los Queules" (35°59'S-72°41'W), located 71 km west of Cauquenes (Fig. 1). This protected area along with private neighbor lands holds one of the largest remnants of Maulino forest of 600 ha. The continuous forest is surrounded by small forest fragments of different sizes (Donoso et al., 2003).

We evaluated seed production of *N. glauca* and *N. obliqua* monthly from March 2002 to March 2009. Seeds were collected in 0.25 m<sup>2</sup> traps held up 1 m above soil level. We selected 20 sampling points in continuous forest and 5 sampling points in each fragment. Each sampling point contained a pair of traps which were considered a single unit of 0.5 m<sup>2</sup> of area. Seed production was quantified as the number of seeds per month or annals.

Pre-dispersal seed-predation was assessed as the percentage of the number of seeds preyed upon regarding the total number of seeds collected per month or year. Preyed seeds showed a hole through the insect larvae emerged.



**Fig. 1.** (A) Geographical distribution of the Maulino forest (grey) and location of Reserva Nacional Los Queules. (B) Study site showing continuous forest and forest fragments (dark gray areas). Other patches of native forest are shown in light gray, and matrix of pine plantations are in white. Dashed line indicates the limits of Reserva Nacional Los Queules (from Donoso et al., 2003: p 65).

#### 2.4 Data analysis

Samples taken in each habitat were considered as replicates. Spatial independence among samples was tested through the Mantel test. Spatial independence was not significant only in 11 of 48 comparisons, for this reason we considered all sampling points from each habitat as spatially independent (Mantel test, 10,000 iterations; Table 1).

Differences in annual seed production and pre-dispersal seed predation between continuous forest and forest fragments for each species, and between species was evaluated through repeated measures ANOVA of two and three ways, respectively, with time (years), habitat and species as factors. Data was rank transformed to normalize distributions and stabilize variance (Conover and Iman, 1981). Data did not meet the sphericity assumption, tested through Mauchly test, therefore we used the Greenhouse–Geisser adjusted probabilities when  $\epsilon$  reach values up to 0.75, and used the Huynh–Feldt adjusted probabilities when  $\epsilon > 0.75$ . Post-hoc comparisons between years and species were performed through the Tukey test.

To test the correlation of seed production and pre-dispersal seed predation between habitats, and between *N. glauca* y *N. obliqua* we run Pearson correlations. To test correlations of seed production with temperature and precipitation, we run Pearson correlations considering annual seed production and the mean of precipitation; average, minimum and maximum temperatures of Chanco meteorological station (Dirección Meteorológica de Chile, 2000-2008) for months of floral primordia development (June-August of the preceding year) and flowering (September-October of the preceding year) of *Nothofagus* genus (Donoso, 1995), all of them described as key periods affecting seed production (Richardson et al., 2005). Finally, we run Pearson correlations to assess the relation of seed production with pre-dispersal seed predation

**Table 1.**

Mantel test to determine spatial independence of samples considering seed production and pre-dispersal seed predation rate for *N. glauca* and *N. obliqua*, between years 2003-2008. \* = data not enough for performing statistical tests.

	<i>N. obliqua</i>				<i>N. glauca</i>			
	Continuous (r, P)		Fragments (r, P)		Continuous (r, P)		Fragments (r, P)	
Seed production								
2003	-0,077	0,934	0,173	0,008	-0,018	0,606	0,096	0,095
2004	0,026	0,307	-0,033	0,666	0,050	0,238	0,296	< 0.0001
2005	0,065	0,098	0,114	0,063	-0,041	0,716	0,008	0,464
2006	0,022	0,348	0,126	0,040	-0,003	0,515	0,180	0,008
2007	-0,024	0,692	0,237	< 0.001	-0,074	0,849	-0,158	0,985
2008	-0,107	0,929	0,413	< 0.0001	0,032	0,326	0,134	0,031
Seed predation %								
2003	-0,051	0,835	-0,122	0,955	0,021	0,389	-0,030	0,654
2004	0,181	< 0.001	0,027	0,356	-0,065	0,817	0,145	0,026
2005	0,035	0,258	0,027	0,350	-0,006	0,543	0,183	0,006
2006	-0,109	0,930	-0,088	0,885	0,072	0,157	-0,073	0,844
2007	0,095	0,030	0,069	0,167	0,077	0,147	*	*
2008	-0,138	0,996	-0,037	0,700	-0,029	0,650	0,073	0,157

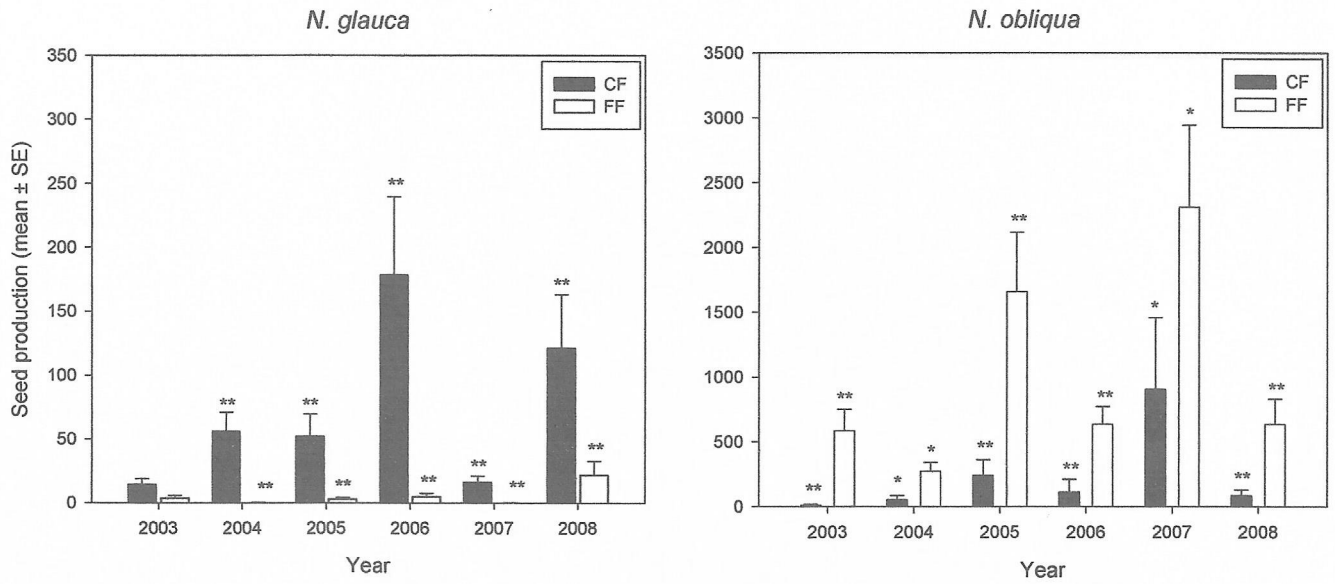
### 3. Results

#### 3.1. Seed production

There was a habitat and time effect on seed production in both species (Table 2). Seed production in continuous forest correlated with production in fragments in both *N. obliqua* ( $r = 0.79$ ;  $P < 0.0001$ ) and *N. glauca* ( $r = 0.34$ ;  $P = 0.001$ ). Seed annual production in *Nothofagus glauca* was significantly higher in continuous forest, except for 2003 when there was no significant differences (Fig. 2). Seed annual production in *Nothofagus obliqua* was significantly higher in fragments for all sampling years (Fig. 2). In average *N. glauca* seed production was 84.5 times higher in continuous forest than forest fragments, whilst *N. obliqua* seed production is 14.7 times higher in fragments than in continuous forests.

**Table 2.** Results of two ways rm ANOVA for forest fragmentation effect (habitat) and year on annual seed production of *N. glauca* and *N. obliqua*.

Source of Variation	d.f	MS	F	P
<i>N. glauca</i>				
Habitat	1	276150	24.24	<0.0001
Year	5	11168	11.44	<0.0001
Habitat x year	5	5271	5.40	<0.001
Error	190	976		
<i>N. obliqua</i>				
Habitat	1	268269	28.44	<0.0001
Year	5	30506	17.50	<0.0001
Year x habitat	5	6429	3.69	0.003
Error	190	1743		



**Fig. 2.** Annual *N. glauca* and of *N. obliqua* seed production during 2003 to 2008 in a continuous forest (CF) and forest fragments (FF) (mean  $\pm$  SE). The asterisk on the bar indicates significant differences of seed production between habitats (\*  $P < 0.05$ ; \*\*  $P < 0.001$ ).

**Table 3.**

Results of Tukey test among years of seed production of *N. glauca* and *N. obliqua* in continuous forest and fragments.

		<i>N. glauca</i>				
		2004 (p)	2005 (p)	2006 (p)	2007 (p)	2008 (p)
Continuous						
	2003	0.002	0.352	<0.001	0.949	<0.001
	2004		0.456	0.715	0.042	0.535
	2005			0.015	0.883	0.006
	2006				<0.001	1.000
	2007					<0.001
Fragments						
	2003	0.117	0.611	0.896	0.045	0.376
	2004		0.935	0.688	0.999	<0.001
	2005			0.995	0.781	0.006
	2006				0.448	0.032
	2007					<0.001
		<i>N. obliqua</i>				
		2004 (p)	2005 (p)	2006 (p)	2007 (p)	2008 (p)
Continuous						
	2003	0.583	<0.001	0.909	<0.001	0.009
	2004		0.043	0.991	<0.001	0.490
	2005			0.006	0.262	0.866
	2006				<0.001	0.171
	2007					0.013
Fragments						
	2003	0.018	0.771	0.972	0.014	1.000
	2004		<0.001	0.001	<0.001	0.009
	2005			0.994	0.379	0.873
	2006				0.126	0.993
	2007					0.027

Seed production varied significantly through years (Table 3). In forest fragments, *Nothofagus glauca* reached productions up to 217 times larger than the year with lower seed production (2008 versus 2007), whereas in continuous forest it was only 12.5 times higher (2006 versus 2003). In *N. obliqua*, between-year variation of seed production was larger in the continuous forest. Difference was 91.5 fold between years of higher and lower seed production (2007 versus 2003), compared to fragments where the largest inter-annual variation was a 8.5 fold difference between years (2007 versus 2004).

Annual seed production of *N. obliqua* from both habitats and of *N. glauca* from continuous forests was not correlated with precipitation, average, minimum and maximum temperatures (Table 4). Annual seed production of *N. glauca* at fragments was negatively correlated with average, minimum and maximum temperature during floral primordia development period and with maximum temperature during flowering period.

**Table 4.**

Results of Pearson Correlations among annual seed production of fragments and continuous forest with precipitation, average, minimum and maximum temperatures of Chanco meteorological station.

	<i>N. glauca</i>		<i>N. obliqua</i>	
	Continuous (r,P)	Fragment (r,P)	Continuous (r,P)	Fragment (r,P)
<u>Floral primordia development</u>				
Precipitation	0.134 ; 0.800	-0.195 ; 0.712	0.189 ; 0.720	0.506 ; 0.306
Temperature				
Average	-0.523 ; 0.287	-0.852 ; 0.031	0.702 ; 0.120	0.623 ; 0.186
Minimum	-0.257 ; 0.624	-0.864 ; 0.026	0.585 ; 0.223	0.495 ; 0.318
Maximum	-0.346 ; 0.502	-0.871 ; 0.024	0.630 ; 0.180	0.515 ; 0.296
<u>Flowering</u>				
Precipitation	-0.291 ; 0.575	-0.579 ; 0.228	0.306 ; 0.556	0.511 ; 0.301
Temperature				
Average	-0.356 ; 0.489	-0.565 ; 0.242	0.638 ; 0.173	0.780 ; 0.067
Minimum	-0.525 ; 0.285	-0.232 ; 0.658	0.339 ; 0.510	0.689 ; 0.130
Maximum	-0.504 ; 0.308	-0.818 ; 0.047	0.609 ; 0.199	0.559 ; 0.249

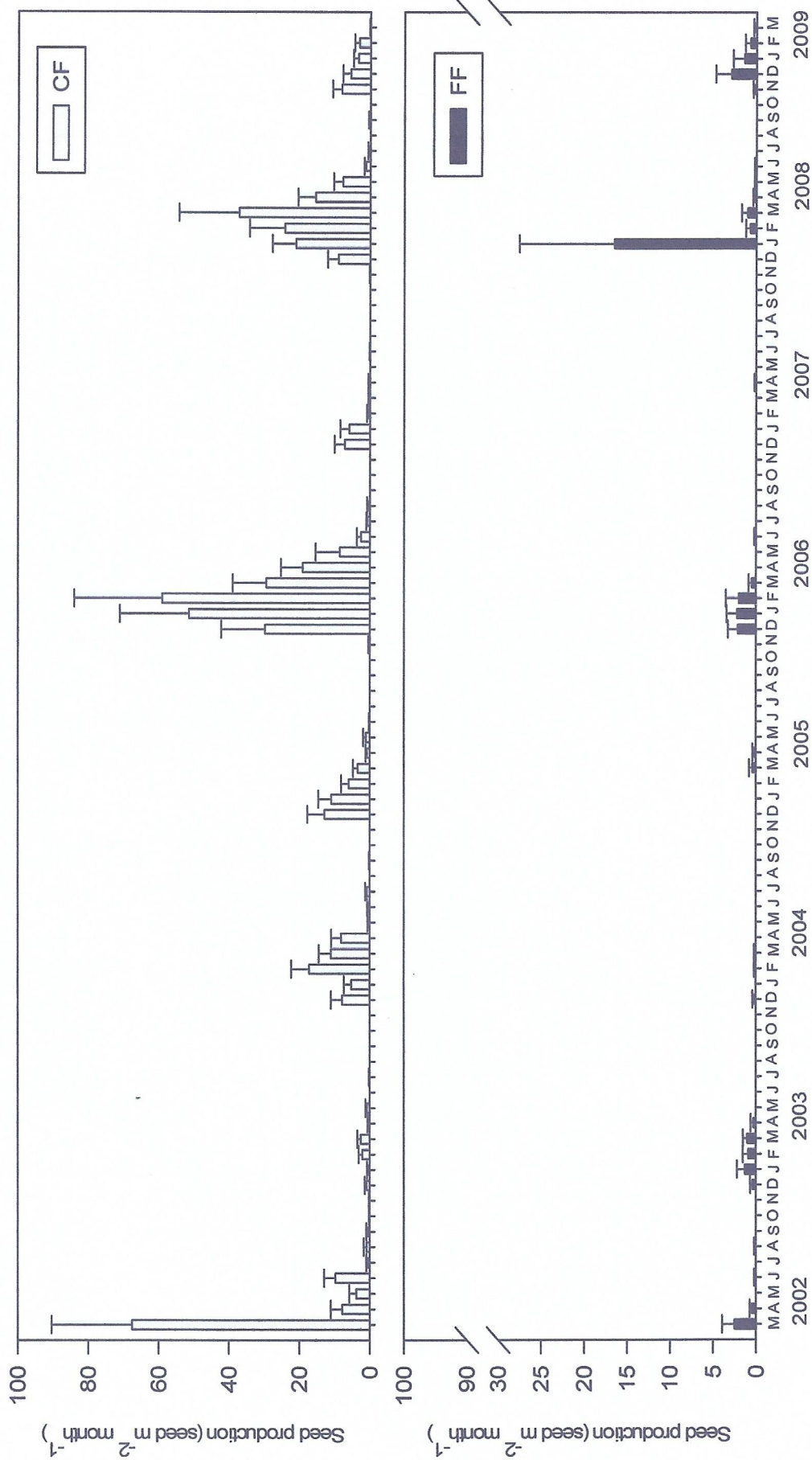


Fig. 3. *Nothofagus glauca* seed production during 2002 to 2009 in continuous forest (CF) and forest fragments (FF) (mean ± SE).



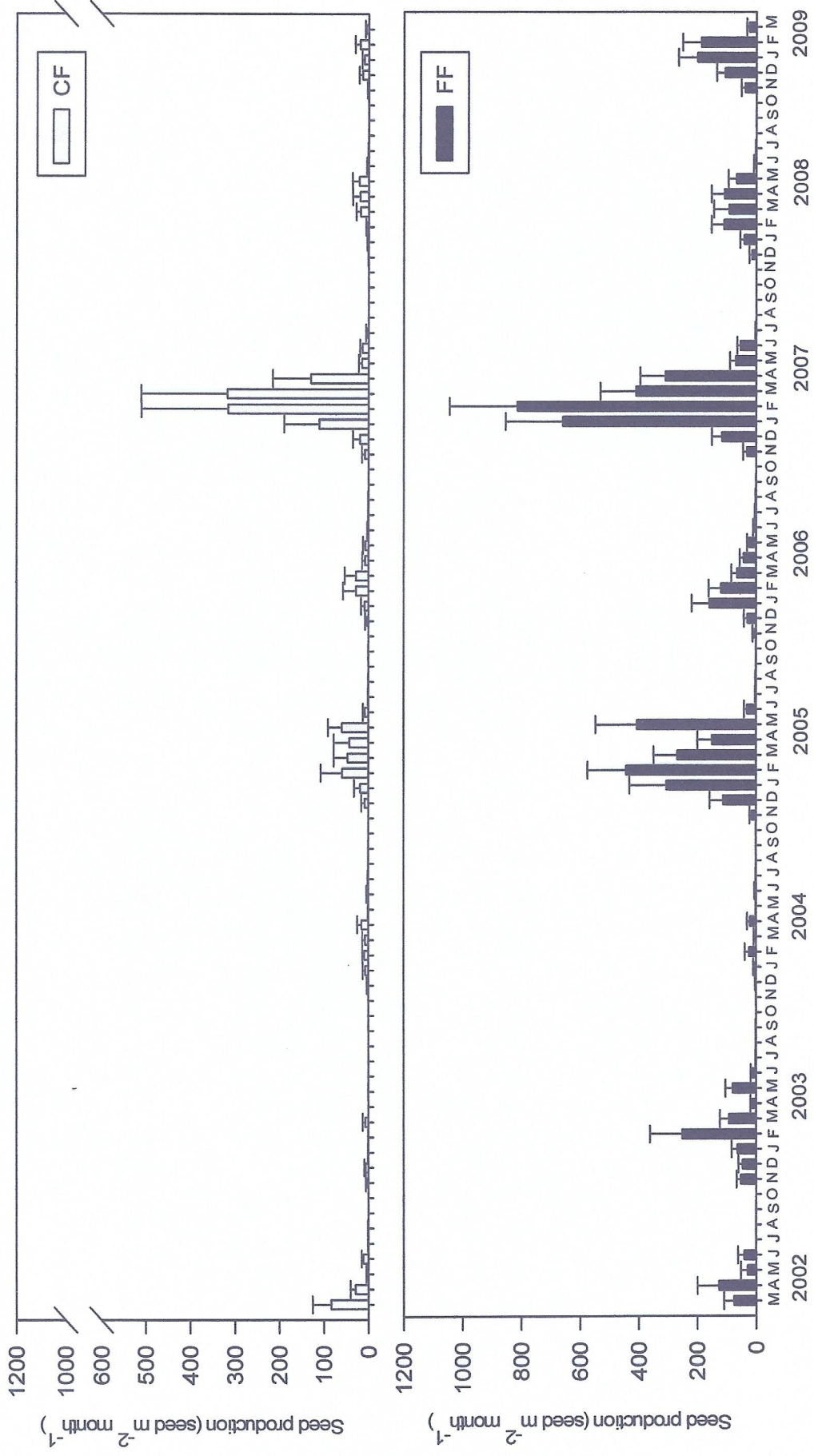


Fig. 4. *Nothofagus obliqua* seed production during 2002 to 2009 in continuous forest (CF) and forest fragments (FF) (mean ± SE).

Annual production was not correlated among species ( $r = -0.063$   $P = 0.42$ ). *Nothofagus glauca* exhibited higher production during December to April (Fig. 3), and *N. obliqua* reached maximum during December to June (Fig. 4). The maximum *N. glauca* annual production occurs every 2 to 4 years, while in *N. obliqua* the maximum of annual production occurs every 2 years. *Nothofagus obliqua* produce significantly more seeds than *N. glauca*.

Seed production differs significantly between species (Table 5). There are a significant year x species effects over seed production (Table 5), thus years of maximum seed production of *N. glauca* differs from those of *N. obliqua*. Seed production of *N. glauca* and *N. obliqua* did not differs for year x habitat and species x habitat x year interactions effects, this means, seed production differences among forest fragments and continuous forest of each species did not vary through time.

**Table 5.**

Results of three ways rm ANOVA for forest fragmentation effect (habitat), species of study and year on annual seed production. If data does not meet sphericity assumption, P values were adjusted using Greenhouse-Geisser adjustment ( $\epsilon = 0.318$ ).

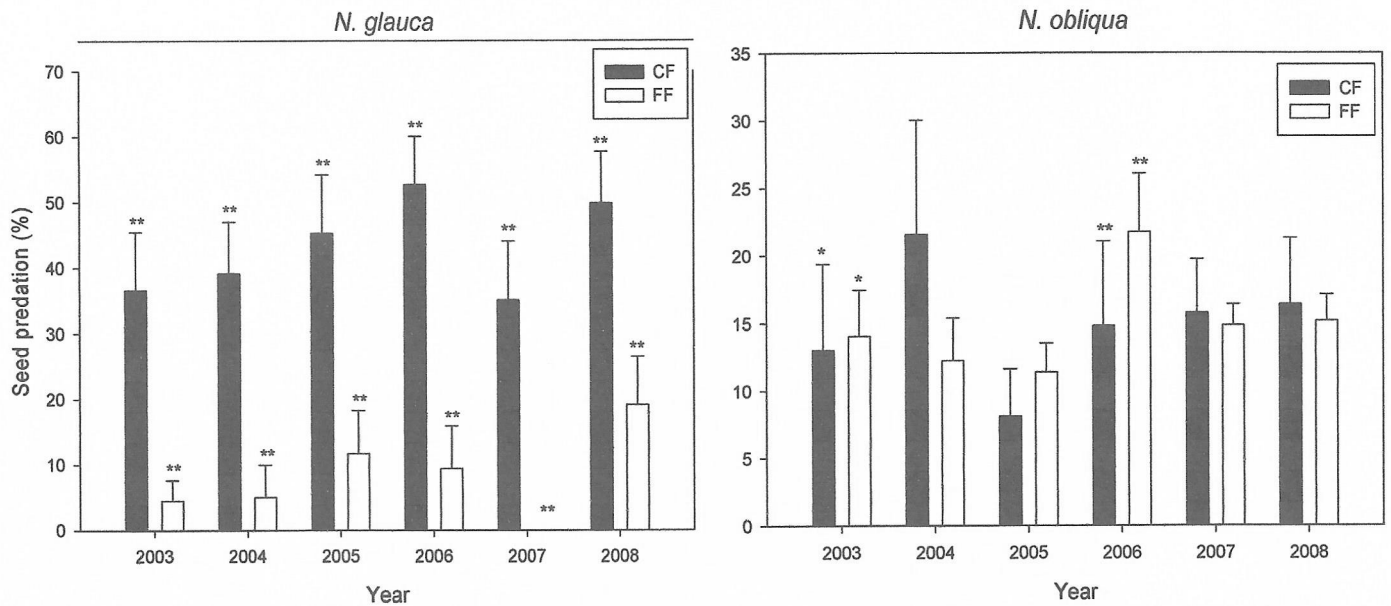
Variation source	d.f	MS	F	P>F	
Intercept	1	787320.0	780.72	< 0.001	
Species	1	39694.2	39.36	< 0.001	
Habitat	1	90.1	0.09	0.766	
Species x habitat	1	52899.0	52.46	< 0.001	
Error	76	1008.5			
					Adj P>F G-G
Year	5	0.0	0.00	1.000	< 0.001
Year x species	5	1849.6	12.43	< 0.001	< 0.001
Year x habitat	5	895.2	6.02	< 0.001	0.082
Year x species x habitat	5	412.4	2.77	0.018	0.118
Error	380	148.8			

### 3.2. Pre-dispersal seed predation

There was a habitat effect on pre-dispersal seed predation in both species (Table 6). Pre-dispersal seed predation in continuous forest was correlated with seed predation at fragments in *N. glauca* ( $r = 0.33$ ,  $P < 0.0001$ ) and in *N. obliqua* ( $r=0.50$ ,  $P < 0.0001$ ). Pre-dispersal seed predation of *N. glauca* was significantly higher in continuous forest than in fragments (Fig. 5; Tukey,  $P < 0.001$ ), reaching 43.1% in *N. glauca* in continuous forest and 8.3% in fragments. Pre-dispersal seed predation in *N. obliqua* was 1.1 and 1.5 times higher in fragments during 2003 and 2006 (Fig. 5).

**Table 6.** Results of two ways rm ANOVA for forest fragmentation effect (habitat), and year on annual pre-dispersal seed predation percentage of *N. glauca* and *N. obliqua*.

Variation source	d.f	MS	F	P>F
<i>N. glauca</i>				
Habitat	1	220160	29.30	<0.001
Year	5	5282	3.04	0.011
Habitat x year	5	595	0.34	0.886
Error	190	1735		
<i>N. obliqua</i>				
Habitat	1	70042	10.04	0.003
Year	5	10112	2.74	0.020
Habitat x year	5	3697	1.00	0.417
Error	190	3685		



**Fig. 5.** Annual *N. glauca* and of *N. obliqua* pre-dispersal seed predation percentage during 2003 to 2008 in a continuous forest (CF) and forest fragments (FF) (mean  $\pm$  SE). The asterisk on the bar indicates significant differences of seed production between habitats (\*  $P < 0.05$ ; \*\*  $P < 0.001$ ).

Annual pre-dispersal seed predation was not correlated among species ( $r = 0.09$ ,  $P = 0.26$ ). Seeds were preyed upon during the entire production period for both species, December to April in *N. glauca* (Fig. 6) and December to July in *N. obliqua* (Fig. 7). *Nothofagus glauca* annual pre-dispersal seed predation differs significantly between 2007 and 2008 (Tukey,  $P = 0.012$ ), years with the lower and higher pre-dispersal seed predation, respectively, at both habitats. Pre-dispersal seed predation in *Nothofagus obliqua* varied significantly between 2003 and 2007 (Tukey,  $P < 0.05$ ). In continuous forest it was significantly higher in 2007 compared to 2003 (Table 7). Pre-dispersal seed predation of *N. obliqua* did not differ through time at forest fragments (Table 7).

**Table 7.** Results of Tukey test among years of pre-dispersal seed predation of *N. glauca* and *N. obliqua* in continuous forest and fragments.

		<i>N. glauca</i>				
		2004 (p)	2005 (p)	2006 (p)	2007 (p)	2008 (p)
Continuous						
2003	1.000	0.948	0.367	0.999	0.502	
2004		0.991	0.553	0.985	0.694	
2005			0.896	0.796	0.958	
2006				0.177	1.000	
2007					0.272	
Fragments						
2003	1.000	0.965	0.997	0.985	0.408	
2004		0.949	0.994	0.991	0.363	
2005			0.999	0.672	0.892	
2006				0.859	0.722	
2007					0.107	

		<i>N. obliqua</i>				
		2004 (p)	2005 (p)	2006 (p)	2007 (p)	2008 (p)
Continuous						
2003	0.921	0.999	0.991	0.046	0.432	
2004		0.987	0.999	0.412	0.956	
2005			1.000	0.115	0.659	
2006				0.204	0.811	
2007					0.91	
Fragments						
2003	0.994	1.000	0.617	0.850	0.867	
2004		0.994	0.271	0.511	0.542	
2005			0.610	0.845	0.867	
2006				0.999	0.998	
2007					1.000	

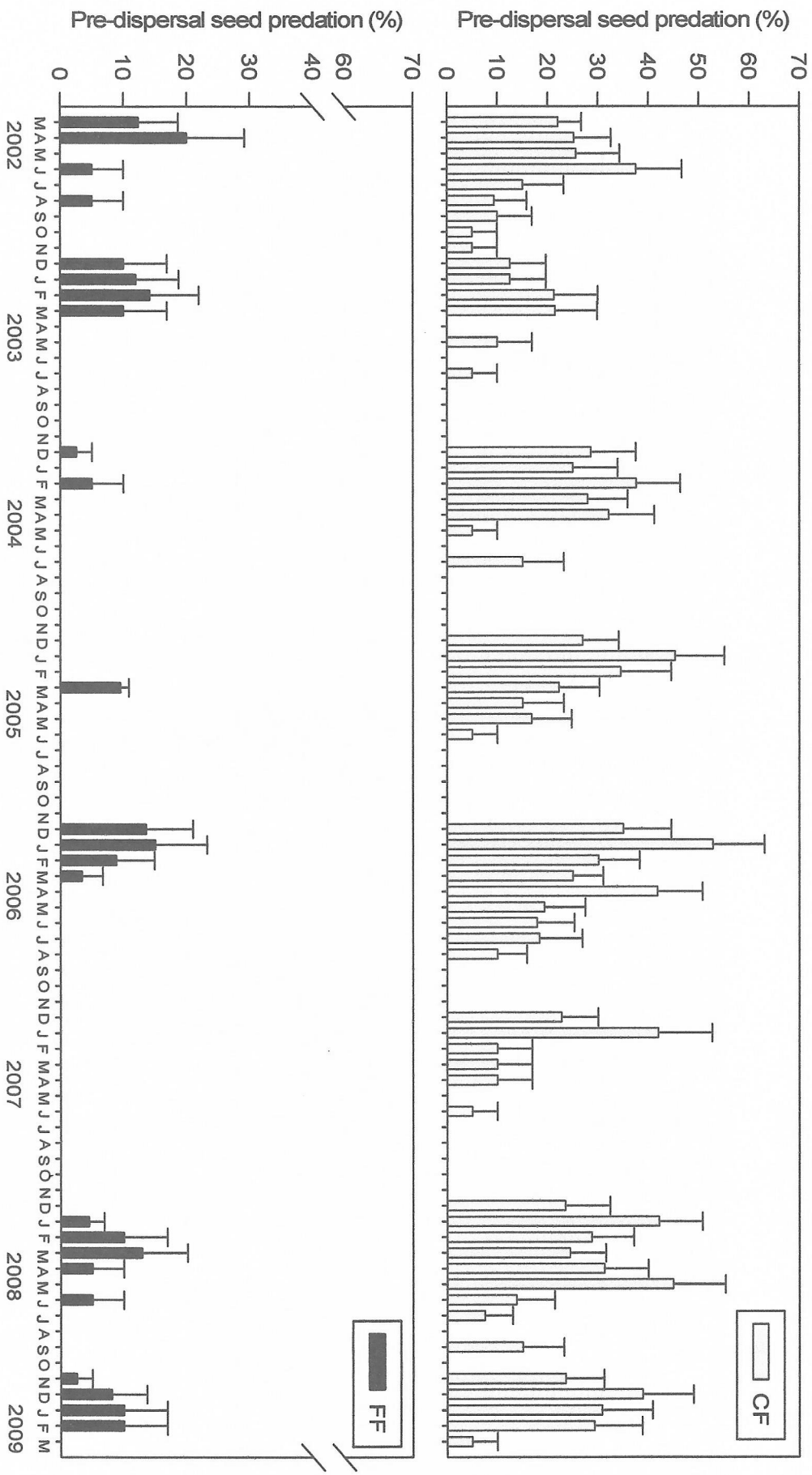


Fig. 6. *Nothofagus glauca* pre-dispersal seed predation during 2002 to 2009 in continuous forest (CF) and forest fragments (FF) (mean  $\pm$  SE).

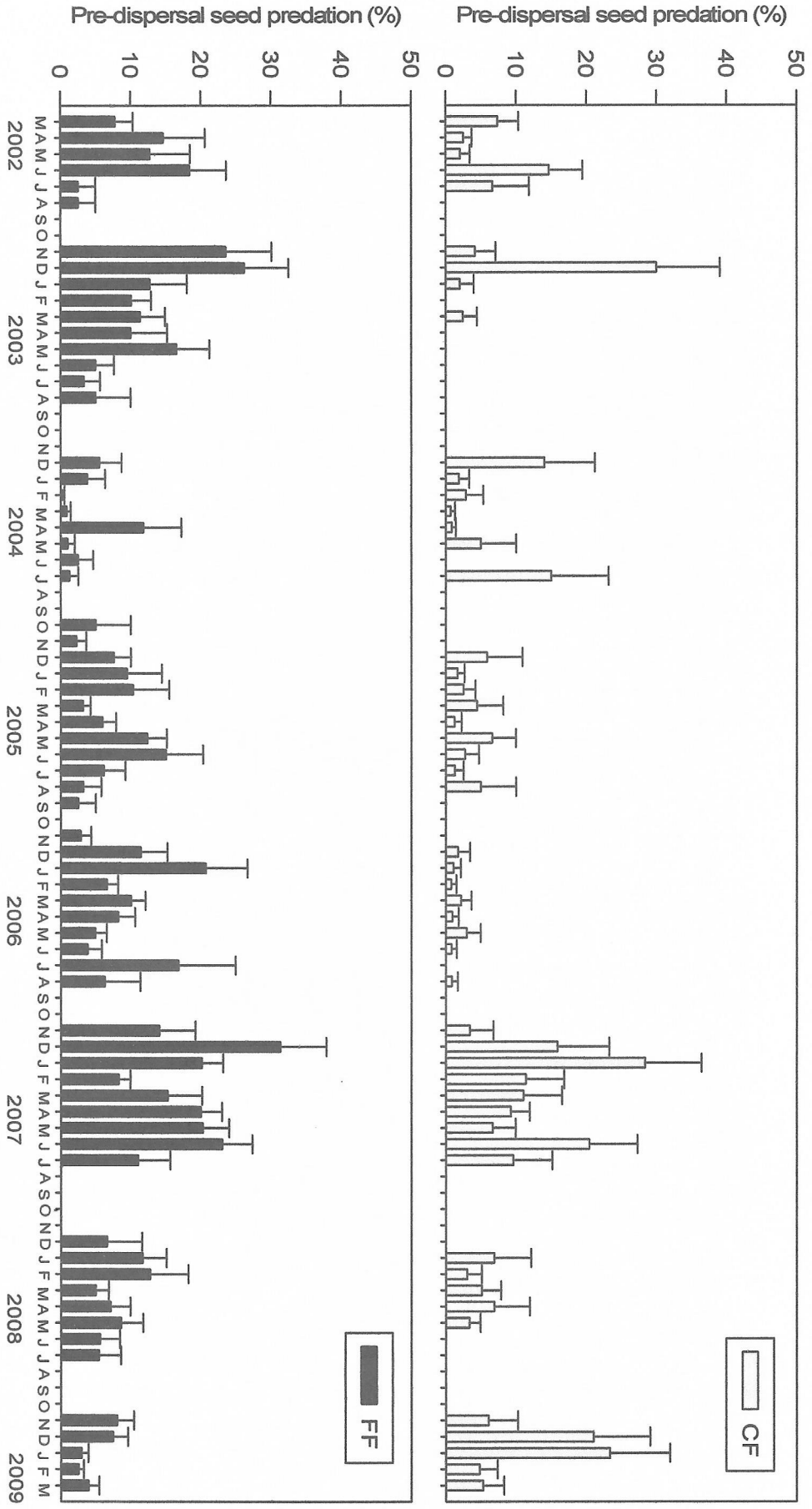


Fig. 7. *Nothofagus obliqua* pre-dispersal seed predation during 2002 to 2009 in continuous forest (CF) and forest fragments (FF) (mean  $\pm$  SE).

Pre-dispersal seed predation percentage of *N. glauca* and *N. obliqua* differs among habitats (Table 8), thus *N. glauca* seeds were more preyed upon in continuous forest and *N. obliqua* seeds were more preyed upon in forest remnants. Nevertheless, there was not significant effects of year x species; year x habitat or year x species x habitat interactions on pre-dispersal seed predation (Table 8), that is, pre-dispersal seed predation differences among habitats for *N. glauca* and *N. obliqua* did not fluctuated significantly through time, and did not varies significantly between both species over time.

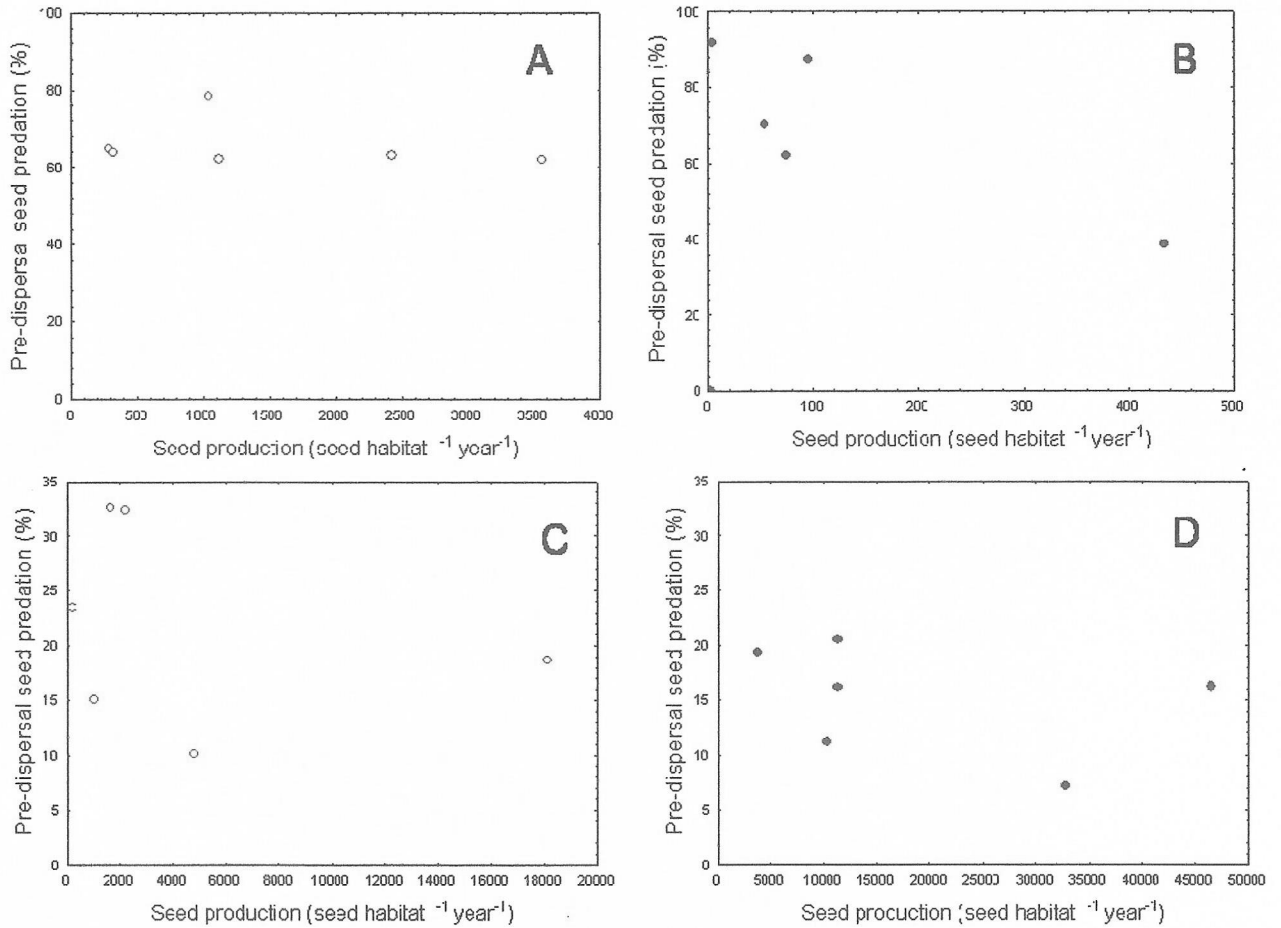
**Table 8.**

Results of three ways rm ANOVA for forest fragmentation effect (habitat), species of study and year on annual pre-dispersal seed predation percentage. If data does not meet sphericity assumption P-values were adjusted using Huynh-Feldt adjustment ( $\epsilon = 0.975$ ).

Variation source	d.f.	MS	F	P>F	
Intercept	1	787320	839.91	< 0.001	
Species	1	1128.5	1.20	0.276	
Habitat	1	8060.6	8.60	0.004	
Species x habitat	1	37188.8	39.67	< 0.001	
Error	76	937.4			Adj P>F H-F
Year	5	0	0.00	1.000	0.071
Year x species	5	1222.5	4.72	< 0.001	0.108
Year x habitat	5	221.8	0.86	0.510	0.950
Year x species x habitat	5	209.5	0.81	0.544	0.628
Error	380	258.9			



There was not correlation among annual pre-dispersal seed predation and annual seed production for *N. glauca* at continuous forest ( $r = -0,29$ ;  $P = 0,58$ ) or fragments ( $r = -0,17$ ;  $P = 0,74$ ) and neither for *N. obliqua* at continuous forest ( $r = -0,27$ ;  $P = 0,60$ ) or fragments ( $r = -0,38$ ;  $P = 0,46$ ) (Fig. 8).



**Fig. 8.** Correlations of annual seed production with annual pre-dispersal seed production percentage of *N. glauca* at continuous forest (A) and fragments (B) and of *N. obliqua* at continuous forest (C) and forest fragments (D).

#### 4. Discussion

Seed production and pre-dispersal seed predation of *Nothofagus glauca* and *N. obliqua* varies with forest fragmentation but this habitat modification does not modify the synchrony of seed production across habitats. This fragmentation effect on seed production of *N. obliqua* and *N. glauca* is supported by the previous *N. glauca* study that also shows differences among continuous forest and fragments for 2005, but not for 2006 (Burgos et al. 2006).

*Nothofagus obliqua* seed production is higher in fragments, being consistent with the raised hypothesis, whereas *N. glauca* does not meet with it, producing more seeds in continuous forest than fragments. Negative correlations among seed production of *N. glauca* and temperature at a regional level during flowering and floral primordia development periods may be enhanced in Maulino forest's fragments, due to microclimatic differences in temperature and humidity regard to continuous forest (Rubio & Simonetti, 2009). Therefore, reduction of seed production of *N. glauca* at Maulino forest's fragments may possibly be explained because the temperature during floral primordia development of *N. glauca* was higher than the minimum temperature optimal for floral primordia development, up to which primordia production decreases and thus seed production, as found in *Fagus crenata* (Kon et al., 2005). The high seed production of *N. obliqua* and the lower seed production of *N. glauca* found in fragments probably are more related to microclimatic factors than to the higher density of individuals in each habitat.

Annual seed production of *N. glauca* and *N. obliqua* evidenced an inter-annual variation during the period 2003-2008. Seed production temporal variation is consistent with findings of previous assessments of *N. glauca* seed production made during 2005 and 2006, observing higher seed production in 2006 than in 2005 (Burgos et al. 2008). The synchrony through time of seed production fluctuations between habitats in *N. glauca* and *N. obliqua*, evidence that seed production probably was determined for a same factor or group of factors

that affects both species. Despite differences of seed production among fragments and continuous forest, they maintain a temporal synchrony between habitats, which differs from what has been described in other organisms such as rodents from a tropical fragmented forest that shows asynchrony among isolated populations (Adler, 1994).

Pre-dispersal seed predation of Maulino forest shows significant differences for some of the sampling years when it was evaluated for each species (2003 and 2006 for *N. obliqua*), therefore the difference of seed predation among habitats is a sporadic phenomenon. Unlike previous studies in *N. glauca*, that describes that pre-dispersal seed predation does not vary significantly among habitats (Burgos et al., 2008), the results of this study indicate that fragmentation would have an effect on pre-dispersal seed predation in some years. Thereby, pre-dispersal seed predation dynamics differs from avian insectivory dynamics described for Maulino forest, which does not differ significantly between years and were the double in fragments respect to continuous forest (Lluch et al., 2009).

Additionally, pre-dispersal seed predation of *N. glauca* and *N. obliqua* in continuous forest and fragments were not correlated with seed production, therefore there is no predator satiation differing from the hypothesis raised. Thus, seeds available to germinate are independent of seed production, so germination depends on other factors such as temperature. Further, non-dependence of pre-dispersal seed predation of seed production found in this study for *N. glauca* and *N. obliqua* differs from that described for other species such as *Fagus crēnata*, for which the intensity of pre-dispersal seed predation is not stable and strongly affected by seed production, decreasing by fluctuations in total seed production between years (Yasaka et al, 2003). In short, there is no single effect of forest fragmentation upon seed production and pre-dispersal seed predation even among closely related species, revealing more complex impacts than hitherto recognized.

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