Agroforest Syst
DOI 10.1007/s10457-016-9999-7

Ten years of seed production and establishment of regeneration measurements in *Nothofagus antarctica* forests under different crown cover and quality sites, in Southern Patagonia

Héctor A. Bahamonde · M. V. Lencinas · G. Martínez Pastur · L. Monelos · R. Soler · P. L. Peri

Received: 6 April 2015 / Accepted: 16 August 2016

Abstract This study evaluated the seed production and quality and the subsequent regeneration establishment in five pure *Nothofagus antarctica* forests growing at different site qualities and crown cover during 10 years, in Southern Patagonia (Argentina). Four traps of 1 m^2 were installed in each stand and sampled monthly (between February and May) each year. The incorporation and survival of seedlings were evaluated using four permanent plots of 1 m^2 in each stand. The site quality of the studied forests did not influence seed production and regeneration. The amount of seed production and seed quality were proved to have a decisive influence on the *N. antarctica* seedling establishment in the subsequent years. At the same time, our results suggest that independently of the site class, the canopy openness for silvopastoral use improved the conditions for seedling establishment. However, the success of seedling survival over time would be conditioned for the influence of other factors such as understory competition.

Keywords Ñire · Silvopastoral system · Seedling survival · Native forest

Electronic supplementary material The online version of this article (doi:10.1007/s10457-016-9999-7) contains supplementary material, which is available to authorized users.

H. A. Bahamonde (✉) · P. L. Peri
Instituto Nacional de Tecnología Agropecuaria (INTA), cc 332, CP 9400 Río Gallegos, Santa Cruz, Argentina
e-mail: bahamonde.hector@inta.gob.ar

H. A. Bahamonde · L. Monelos · P. L. Peri
Universidad Nacional de la Patagonia Austral (UNPA), Lisandro de la Torre 1070, CP 9400 Río Gallegos, Argentina

M. V. Lencinas · G. Martínez Pastur · R. Soler · P. L. Peri
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

M. V. Lencinas · G. Martínez Pastur · R. Soler
Centro Austral de Investigaciones Científicas (CADIC), Houssay 200, 9410 Ushuaia, Tierra del Fuego, Argentina

Introduction

Nothofagus genus dominates the temperate forests of southern Argentina and Chile (Veblen et al. 1996). Particularly, the deciduous *Nothofagus antarctica* (G. Forster) Oerst. (ñire, ñirre) is present in the broadest ecological amplitude, from sea level to 2000 ma.s.l. and from 36°30′ to 56°00′ SL (Donoso et al. 2006), with a high morphological variability in their populations (Ramírez et al. 1985; Steinke 2004), some of which have been shown to be correlated with neutral genetic variation (Premoli and Steinke 2008; Steinke et al. 2008). Also, there are studies along its entire latitudinal range showing that *N. antarctica* is highly polymorphic for different molecular markers (Acosta et al. 2012).

In southern Argentinean Patagonia (Santa Cruz and Tierra del Fuego provinces) ñire forests occupy 431,000 ha (Collado 2001; Peri and Ormaechea 2013), in a great variety of environmental conditions (water balance, temperature gradient and soil qualities), which derived in different stand site qualities. Related to this, Ivancich et al. (2011) have proposed a classification of site qualities for ñire forests in southern Argentinean Patagonia, which is based on site index equations. In Santa Cruz province 97 % of ñire forests are growing in site classes (SC) with dominant trees less than 12 m (Peri and Ormaechea 2013). Also, according to the new Argentinean National Law of minimum environmental standards for native forests (Law N° 26331), 70 % of *N. antarctica* forests in southern Argentinean Patagonia can be used as silvopastoral systems. This implies removal of trees to increase forage production, introduction of cattle and/or sheep into these forests, which could modify different ecological and productive conditions (Bahamonde et al. 2012; Peri and Bahamonde 2012, 2013). In this context, it is essential to know the regeneration dynamics of these forests with focus on its silvopastoral use and growing in different environmental conditions (site quality classes) to ensure the continuity of arboreal stratum (Peri et al. 2009). There are antecedents indicating a negative effect of cattle on the regeneration of trees and shrubs (Raffaele and Veblen 2001) and *N. antarctica* (Echevarria et al. 2012). The information about this issue in Southern Patagonia has been partially addressed both at temporal and spatial scales. Bahamonde et al. (2011) published data about ecological aspects of the regeneration in primary forest (PF); Soler et al. (2013) studied the different stages of the regeneration cycle (pre- and post- dispersal drivers) in a 3 years study of different managed and unmanaged forests, reporting that thinned forest produced lesser male and female flowers than forests with higher crown cover; and Bahamonde et al. (2013a) evaluated the regeneration under silvopastoral uses. However, some crucial gaps still remains unstudied. For this, the objective of this work was to answer the following questions: (1) Does the differences in site quality imply differences in the seed quantity and quality and the subsequent regeneration rate? (2) Does tree removal for silvopastoral use decrease the seed production and the subsequent regeneration establishment? (3) This thinning effect have the same magnitude at different site qualities stands? (4) How the silvopastoral use modify the regeneration pattern compared to unmanaged forests? Based on these questions, we hypothesized: (1) Seed production, quality and subsequent regeneration rate in *N. antarctica* forests is more successful in better site quality classes (2) The annual seed production and quality for a same site quality class is related to the crown cover of the stands, but the opposite may occur with the establishment of seedlings and its survival.

Materials and methods

Study sites

The study sites were located in five pure *N. antarctica* stands in the southwestern of the Santa Cruz province (Patagonia, Argentina) as part of PEBANPA network (Biodiversity and Ecological Long Term Plots of Southern Patagonia, Peri et al. 2014). Three stands were PF with not previous management growing at three different site qualities. The site quality of the stands was determined according to the previous classification of Ivancich et al. (2011), where these authors established five site classes based on models that used the total height of dominant mature trees (H) as indicator of productivity. The site classes of the stands studied here were as follow: site class III (SCIII) where H reached to 11.7 m (51°13′21″SL–72°15′44″WL), site class IV (SCIV) where H reached to 8.0 m (51°13′22″SL–72°15′32″WL) and site class V (SCV) representing a marginal site in the limit with the Patagonian steppe reaching a H of 5.0 m (51°19′05″SL–72°10′47″WL). The other two stands were located adjacent to the SCIV and SCV, respectively, but these were thinned 41 years ago. This allows the comparison between forest with its original crown cover (here after we refer to as PF) and silvopastoral use in the same site quality. The average age of the dominant trees in height ranged between 90 and 100 years. More detailed information about climate, soil and structural characterization of stands is available in Bahamonde et al. (2015).

Seed production and quality

To quantify the seed production four traps of 1 m^2 were installed in each stand (randomly distributed in the PF and regularly separated in the silvopastoral stands) 1 m above the ground. The traps were sampled monthly during the period of seed fall at these latitudes (February–May) (Bahamonde et al. 2011) during a continuous period of 10 years (2004–2013). The collected material was carried to the laboratory in plastic bags and then, the seeds were quantified manually. For each stand the mean annual seed production per unit area (millions ha^{-1}) was calculated by summing the monthly values.

Seeds size was calculated weighting all seeds with an analytical balance (±0.001 g) to determine the weight of 1000 seeds. Also, three to five samples of 100 seeds (depending on the availability of seed each year) were randomly taken for each stand to quantify the percentage of seed germination. For this, the selected seeds were stratified at 4 °C for 60 days (Premoli 1991), then, the stratified seeds were placed in a germination chamber according to ISTA (1999) standards for *Nothofagus* spp. for a period of 60 days. The counting of seedlings was carried out every 2 days. We consider a successfully germinated seedling when two cotyledons were full developed.

Regeneration

To quantify the incorporation of seedlings in each stand, four permanent plots of 1 m^2 (1 × 1 m) were installed, and each individual seedling was located in a XY coordinates system. Half of the permanent plots were closed with wire mesh to avoid wild and domestic animals browsing on regeneration. In each plot, the number of seedlings incorporated (December) and its mortality during growth season (April) were measured. These dates have been documented as adequate to evaluate the effective new regeneration in a given year (Bahamonde et al. 2011).

The volumetric water content (0–20 cm) was measured in each stand using a soil moisture meter Time Domain Reflectometry proven precision equipment (TDR flag Eijkelkamp, Model FM-3-14.62, Santa Barbara, USA), in two ways: (a) at the beginning of the growing season (during the last week of November each year from 2005 to 2011) to evaluate water conditions for seedling establishment; and (b) each month from November to April in order to relate the soil water content with the seedling survival.

Data analysis

Exploratory testings were carried out to verify the compliance with the assumptions of normality, homoscedasticity and independence of data for each evaluated condition. While the Shapiro–Wilk test was performed to verify the normality of the data, the Levene test was used to verify homoscedasticity. The independence was verified by analysing residuals from graphs. To evaluate the incidence of site class on seed production, seed weight, germination and temporal distribution of seeds fallen, the three PF stands were analysed with repeated measures ANOVAs with site class as an inter-subject factor, and years as an intra-subject factor. To analyse the seed production and quality (seed weight and germination) and its temporal distribution between crown cover, silvopastoral and PF stands were compared at two site classes through repeated measures ANOVAs with site class and crown cover as inter-subject factors, and years as an intra-subject factor. This type of analysis has been shown to be appropriate for studies like this where data obtained are not independent in time (Gurevitch and Chester 1986). Then, when F-values were significant ($p < 0.05$) a Tukey test was performed for media comparisons. To avoid misinterpretations multiple comparisons were made when the interaction between factors were significant (Willems and Raffaele 2001). With the aim of evaluate the possible incidence of an environmental variable related to the seedling establishment and mortality, the volumetric soil moisture between crown cover was analysed with one-way ANOVA and Tukey test. The installation and survival of seedlings were analysed with the no parametric Kruskal–Wallis test because the data were not normally distributed and the U Mann–Whitney test when significant differences were found.

Finally, to evaluate potential correlations between different evaluated variables (amount, weight and germination of seeds; litterfall production; total volume, crown cover and dominant percentage of trees; volumetric soil moisture; seedling installation and survival) Pearson correlation coefficient was calculated for the five studied stands for the ten evaluated years. Also, the litterfall production evaluated in the same stands during the same years and their structure variables (Bahamonde et al. 2015), were used as others independent variables to evaluate these correlations.

Table 1 Repeated measures ANOVA for seed production, weight and seed germination, measured at three site classes (III, IV and V), and 10 years (2004–2013) in primary *N. antarctica* forests

Source	*df*	Seed production F (p)	Seed weight F (p)	Seed germination F (p)
Between subject effects				
Site class (SC)	2	1.05 (0.394)	26.50 (0.001)	317.36 (<0.001)
Within subject effects				
Year (Y)	9	12.35 (<0.001)	6.12 (<0.001)	74.78 (<0.001)
Interactions				
SC × Y	18	4.21 (<0.001)	3.43 (<0.001)	74.96 (<0.001)

Results

Seed production and quality in PF

Seed production did not differ between PF growing at different site classes (Table 1), with an average production during 10 years of 17, 20 and 11 million seeds ha^{-1}, in SC III, IV and V, respectively. But, both the seed production between years and the interaction between SC and year were significantly different (Table 1). Higher seed production occurred during 2005, 2008 and 2012, while the year 2004 showed the lowest values (Fig. 1a). However, the interaction between years and site classes indicated that maximum seed production not always occurs at the best SC. In example, during 2005 PF in SCIII produced more seeds, but in 2008 this occurred in SCIV (Fig. 1a).

The seed weight varied significantly between SC and year, as well as the interaction between SC and years (Table 1). In the 10 years average the weight of seeds showed a gradient with 1.4, 1.2 and 1.0 g 1000 $seeds^{-1}$ for SC V, IV and III, respectively. Despite this there was a trend of higher seed weight values when differences between site classes occurred (Fig. 1b).

Similarly, the differences of seed germination between SC, years and its interaction were significant (Table 1). The seed germination averaged 9.2, 2.4 and 2.9 % in the evaluated period for SC (V, IV and III), respectively, being significantly greater in SCV, with no differences among SCIV and SCIII. Comparing the seed germination between SC in each year, it was remarkably higher in SCV during the year 2008 (Fig. 1c).

When we analyzed the percentage of fallen seeds at each month, not differences were found between years ($p > 0.05$) and between SC. A total annual seed production of 40 % occurred in February and declined to <10 % in April (see Supplementary Material).

Changes in seed production and quality due to thinning

The seed production was not modified by the crown cover, but did vary according to the site class and year (Table 2). During the 10 years evaluated period the PF averaged 20 million seeds ha^{-1} and the silvopastoral (SP) stands 13 million seeds ha^{-1} in SCIV, while in SCV the PF and SP stands averaged 11 and 9 million seeds ha^{-1}, respectively. Comparing each year among different crown cover there were significant differences during 2005 and 2006 in stands growing at SCIV with greater values in the PF (see Supplementary Material). In SCV there was different production of seeds only in the year 2013 with major values in PF. The interaction between site class and year is due to the maximum seed production differed between SCIV (2012) and SCV (2008). Similarly to what occurred in PF, the percentage of fallen seeds at each month decreased from 43 % in February to less than 8 % in April without differences between years ($p > 0.05$) and between SC (see Supplementary Material).

The seed weight only varied between years with not significant interactions between the main factors (site quality class, crown cover) (Table 2). Analyzing separately each SC every year, in SCIV there were differences between crown cover during 2 years (2006 and 2009) with major values in PF, while in SCV the seed weight was higher in SP only one of the 10 years (2006) (Table 3).

In the case of seed germination the differences were significant for all factors (Table 2). According site class, the percentage of seed germination was higher

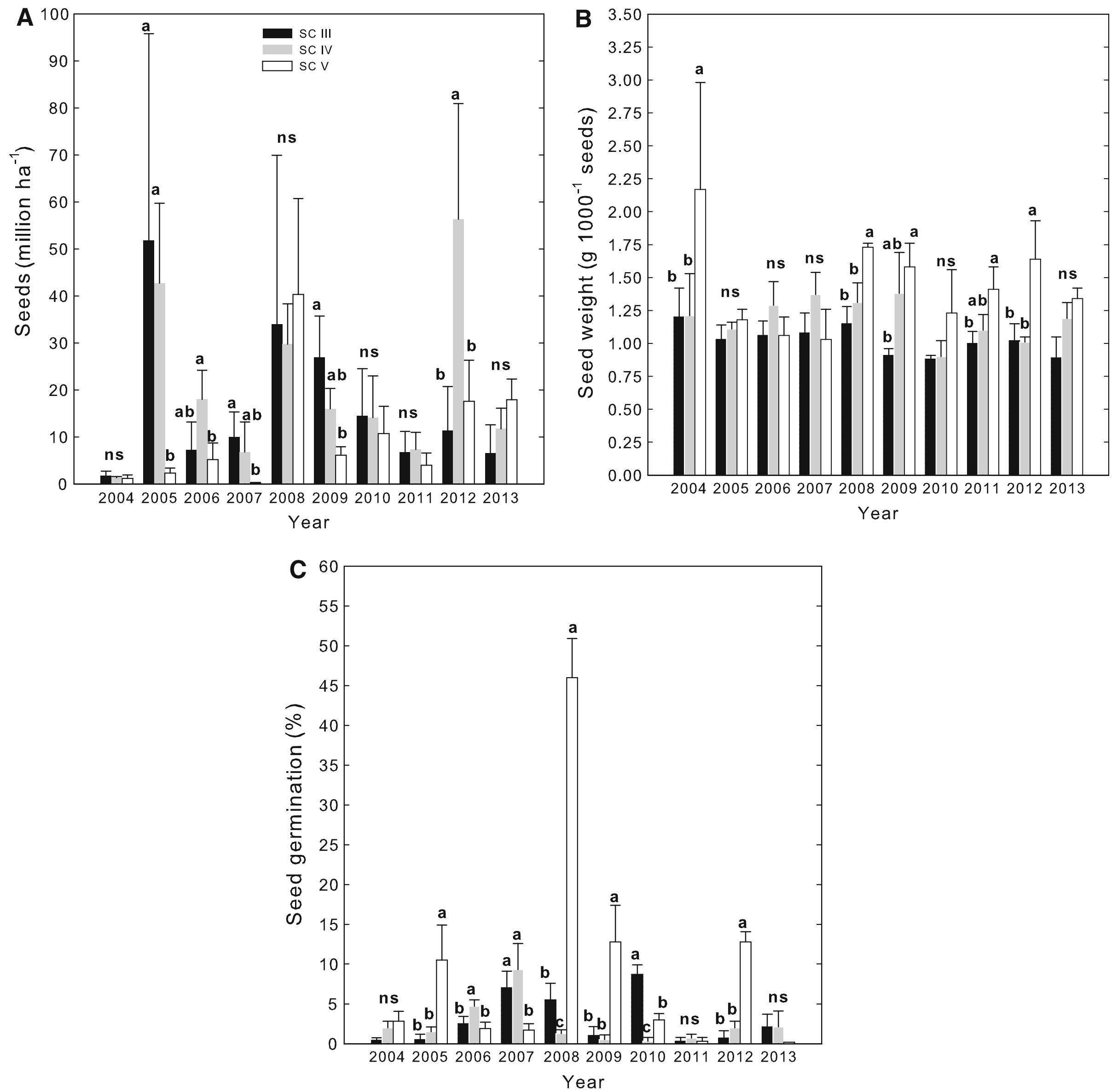

Fig. 1 Seed production (**a**), seed weight (**b**) and seed germination (**c**) measured during 10 years in three primary *N. antarctica* forests growing at different site classes (SC). *Bars* represent the standard error of the mean. *Different letters* among *columns* indicate significant differences among SC ($p < 0.05$). *Ns* not significant differences

in SCV (10.5 %) than in SCIV (2.6 %). According the crown cover SP showed higher values (7.3 %) than PF (5.8 %). Finally, according years of study, the percentage in 2008 was higher (20.3 %) than the other years (ranged from 1.2 to 9.6 %). The interactions were significant among all factors (Table 2). In the stands growing at SCIV the seed germination was higher at SP in 2 years (2010 and 2011), while in SCV the differences among crown cover alternated among years (Table 3).

Regeneration in PF

No differences were found in the seedling installation between the plots with or without wire mesh protection against herbivores ($p > 0.05$). Therefore these results

Table 2 Repeated measures ANOVAs for seed production, weight and seed germination estimated for two site classes (IV and V), two crown cover (PF and silvopastoral stand) and 10 years (2004–2013) in *N. antarctica* forests

Source	*df*	Seed production F (p)	Seed weight F (p)	Seed germination F (p)
Between subject effects				
Site class (SC)	1	5.59 (0.042)	4.55 (0.062)	519.90 (<0.001)
Crown cover (CC)	1	2.85 (0.146)	0.002 (0.97)	18.40 (0.001)
Within subject effects				
Year (Y)	9	19.80 (<0.001)	2.77 (0.007)	75.90 (<0.001)
Interactions				
SC × CC	1	1.31 (0.282)	0.142 (0.72)	12.0 (0.005)
SC × Y	9	11.27 (<0.001)	0.82 (0.602)	76.80 (<0.001)
CC × Y	9	1.82 (0.077)	1.17 (0.329)	16.37 (<0.001)
SC × CC × Y	9	0.91 (0.520)	0.74 (0.674)	22.03 (<0.001)

Table 3 Seed weight and seed germination evaluated in *N. antarctica* primary forest (PF) and silvopastoral (SP) stands growing at SCIV and SCV during 10 years

Year	Seed weight (g 1000^{-1} seeds)				Seed germination (%)			
	SC IV		SC V		SC IV		SC V	
	PF	SP	PF	SP	PF	SP	PF	SP
2004	1.2 (0.3)a	2.0 (1.5)a	2.2 (0.8)a	2.1 (1.0)a	2.0 (0.8)a	2.2 (0.2)a	2.8 (1.3)a	3.1 (0.2)a
2005	1.1 (0.1)a	0.9 (0.1)a	1.2 (0.1)a	1.9 (1.5)a	1.5 (0.6)a	1.5 (0.6)a	10.5 (4.4)a	4.5 (4.2)b
2006	1.3 (0.2)a	1.0 (0.1)b	1.1 (0.1)a	1.6 (0.3)b	4.7 (0.8)a	1.9 (0.8)a	1.9 (0.8)b	25.0 (8.2)a
2007	1.4 (0.2)a	1.8 (1.3)a	1.0 (0.2)a	1.6 (1.0)a	9.3 (3.3)a	9.0 (2.9)a	1.7 (0.8)b	18.3 (6.3)a
2008	1.3 (0.2)a	1.1 (0.2)a	1.7 (0.1)a	1.6 (0.3)a	1.3 (0.5)a	2.3 (1.0)a	46.0 (4.9)a	32.3 (2.1)b
2009	1.4 (0.3)a	0.9 (0.2)b	1.6 (0.2)a	1.1 (0.3)a	0.5 (0.6)a	1.0 (0.8)a	12.8 (4.6)a	2.5 (0.6)b
2010	0.9 (0.1)a	0.8 (0.1)a	1.2 (0.3)a	1.1 (0.3)a	0.3 (0.5)b	4.7 (0.9)a	3.0 (0.8)b	6.7 (4.5)a
2011	1.1 (0.1)a	0.9 (0.1)a	1.4 (0.2)a	1.0 (0.5)a	0.7 (0.5)b	1.7 (0.5)a	0.3 (0.5)b	2.0 (0.8)a
2012	1.0 (0.1)a	0.9 (0.1)a	1.6 (0.3)a	1.5 (0.3)a	2.0 (0.8)a	0.7 (0.9)a	12.8 (1.3)b	20.0 (2.9)a
2013	1.2 (0.1)a	1.0 (0.1)a	1.3 (0.1)a	1.3 (0.6)a	2.1 (2.1)a	2.4 (0.5)a	0 b	4.4 (2.2)a

Numbers in parentheses are the standard deviation of the mean

Among PF and SP for a same year and site class, means followed by the same letter do not differ significantly ($p > 0.05$)

were unified and are presented all together (with and without protection) for each stand. Comparing different site classes of PF, the seedling installation depended on the year. In 2006 seedling installation only occurred in SCIII (10,000 seedling ha^{-1}) with 100 % of mortality at the end of the growing period (April). In 2008 there were 5000 and 180,000 seedlings ha^{-1} in SCIII and SCV, respectively ($p < 0.05$). The survival was 100 % in SCIII and 19 % in SCV at the end of period ($p < 0.05$), but the mortality was 100 % at the second year in both stands. In SCIV the seedling installation was not recorded in any of the evaluated years. Similarly in the others evaluated years there were not seedlings in none of the stands.

Changes in regeneration due to thinning

As was described before for PF the regeneration was also independent of protection against domestic or wild large herbivorous. In SCIV seedling installation only occurred in SP stand, therefore it was not possible to conduct statistical comparison among different crown cover. The establishment of seedlings occurred during 4 years, with 33,000, 8000, 8000 and 5000 seedlings ha^{-1} during 2004, 2007–2009, respectively. Only during the year 2008 there was 67 % of seedling survival at the end of the summer, but at the second year all seedlings did not survive the first growing season. In SCV seedling installation occurred in SP stand during the years 2004, 2008 and 2009 with 63,000, 240,000 and 20,000 seedlings ha^{-1}, respectively. At the end of the growing season there was survival of 39 and 75 % during the years 2008 and 2009, respectively. In 2008 the PF stand had an establishment of 180,000 seedlings ha^{-1}, with not differences ($p > 0.05$) with the equivalent SP stand. However, the survival at the end of the season was lower ($p < 0.05$) in the PF stand with 19 %. Nevertheless, in all cases the seedlings did not survive a second year.

Soil moisture did not change between PF and SP neither at the beginning (November) and the average for the entire growing season (November to April) in the two studied site quality classes (see Supplementary Material). However soil moisture differed between years in both site classes ($p < 0.05$), being higher during the season 2005–2006 than the other years.

Correlation between structural, environmental and seeds

Seedlings establishment was significantly and positively associated to the seed production and its quality (e.g., seed weight and seed germination; Table 4). However, the seedling survival was not correlated with any of the evaluated variables. The seed germination was positively correlated with the seed weight. With regard to the structural variables, the total volume of the stand was positively correlated with the litterfall production and crown cover, but negatively associated to the seed weight, seed germination and % of dominant trees. Also, the % of dominant trees was negatively correlated with the litterfall production and crown cover (Table 4). This last variable was also positively associated to the litterfall production and soil moisture average during the seedling growth season. Finally, the litterfall production was negatively correlated with the soil moisture during the seedling installation.

Discussion

The seed production and quality, establishment and survival of seedlings evaluated are discussed regarding the potential influence of the environmental conditions and management of *N. antarctica* forests. In general, in the studied sites the site quality did not influence their seed production and regeneration. However, the management for silvopastoral use showed some incidence in the regeneration.

Seed production and quality in PF

The seed production was in the range of the reported by Soler et al. (2013), in a primary *N. antarctica* forest of similar structural features to our SCIII stand, evaluated during 3 years in Tierra del Fuego. Although the evaluation of seed production in *Nothofagus* spp. in general, and for *N. antarctica* in particular, are scarce, the great inter annual variability has been reported. Allen et al. (2014) measured seed production in *Nothofagus solandri* forests in New Zealand during 45 years and reported great inter annual variation with values between 0 and more than 10,000 seeds m^{-2}. In a shorter study Marchelli and Gallo (1999) found significant inter annual variation in seed production of *Nothofagus nervosa* in Chile and Argentina. These variations have been related with some type of periodicity in the seeding of the species, which would imply some "special" years with very high production also known as "mast seeding" (Herrera et al. 1998) occurring at certain intervals of years or periodicity. But, strictly there are not antecedents for *Nothofagus* spp. in support of such fixed periodicity. In this study, although we recorded some years with very high seed production, we could not glimpse the mentioned periodicity.

Previous studies in temperate forests around the world have suggested various weather conditions as cues for *masting* depending on tree species and areas (Kelly and Sork 2002; Richardson et al. 2005; Masaki et al. 2008). For *Fagus* sp. forests in Japan, lower temperature in spring and higher temperature in summer and seed fall density in a year were proved to have a decisive influence on the seed fall density in the subsequent year (Masaki et al. 2008). For *N. solandri* forests in New Zealand, Richardson et al. (2005) reported that high seed production was related to cool summers with high soil moisture, warm summers during flower primordia development, and low net C availability. Actually in these same stands studied here, Bahamonde et al. (2011) found an inverse relationship ($p < 0.001$) between seed production and the number of days with air temperature bellow 0 °C during late winter (previous flowering period). However, such weather conditions should be

Table 4 Pearson correlation coefficient (R) and significance (p value) between different parameters in five *N. antarctica* stands under different crown cover and growing in three different site classes

	Seed production	Litterfall production	Seed weight	Seed germination	Total volume	Dominant trees (%)	Seedling installation	Crown cover	SMB	SMA	Seedling survival
Seed production	1										
Litterfall production	0.18 (=0.224)	1									
Seed weight	0.17 (=0.230)	0.22 (=0.123)	1								
Seed germination	0.24 (=0.093)	**−0.34 (=0.016)**	**0.42 (=0.002)**	1							
Total volume	0.22 (=0.132)	**0.69 (<0.001)**	**−0.48 (<0.001)**	**−0.38 (=0.008)**	1						
Dominant trees (%)	0.06 (=0.680)	**−0.48 (<0.001)**	0.09 (=0.538)	0.08 (=0.565)	**−0.40 (=0.004)**	1					
Seedling installation	**0.49 (=0.004)**	0.19 (=0.285)	**0.40 (=0.021)**	**0.74 (<0.001)**	0.29 (=0.099)	0.086 (=0.634)	1				
Crown cover	0.18 (=0.206)	**0.74 (<0.001)**	0.11 (=0.459)	0.15 (=0.288)	**0.47 (=0.001)**	**−0.77 (<0.001)**	0.07 (=0.695)	1			
SMB	0.24 (=0.214)	**−0.44 (=0.020)**	0.14 (=0.472)	0.24 (=0.228)	0.19 (=0.326)	0.12 (=0.547)	0.16 (=0.479)	0.25 (=0.205)	1		
SMA	0.62 (=0.192)	0.45 (=0.365)	0.43 (=0.390)	0.73 (=0.103)	0.01 (=0.989)	−0.80 (=0.055)	0.51 (=0.302)	**0.82 (=0.044)**	0.54 (=0.269)	1	
Seedling survival	0.27 (=0.521)	0.53 (=0.181)	0.57 (=0.142)	0.01 (=0.994)	0.33 (=0.433)	0.21 (=0.623)	0.05 (=0.915)	0.11 (=0.798)	0.67 (=0.143)	0.04 (=0.940)	1

The significant correlations ($p < 0.05$) are showed in bold

SMB soil moisture at the beginning of growth season, *SMA* averaged soil moisture for the entire growth season infrequent enough to provide the above mentioned masting periodicity. This fact can explain the complexity of the process and may clarify why not differences were found in the seed production between the studied stands growing at different site quality classes, associated with contrasting total wood volume (Lencinas et al. 2002), understory productivity (Bahamonde et al. 2012) or litterfall production (Bahamonde et al. 2015).

The range of seed size (evaluated through weight of 1000 seeds) found in this study is similar to the informed in other publications for *N. antarctica* (Premoli 1991), but still being one of the most small of the south American *Nothofagus* spp. with *N. nitida* (Donoso and Escobar 2006). Despite inter annual variations, the trend was that stands in SCV had heavier seeds than SCIV. The factors that determine this trend are not clear, but there are antecedents relating the seeds size to genetic variations (Pastorino and Gallo 2000), environmental effects during development of mother plants (Leishman et al. 2000) or forest structure (Henríquez 2004).

In general, the germination of *N. antarctica* is known as one of the lowest among south American *Nothofagus* spp. (Donoso et al. 2006). Similarly, the variation between years and stands also has been reported for the species in northern latitudes (Premoli 1991). Also, this author found that a population that produced highest percentage of germination had also the heaviest seeds and suggested that these results could be related to optimum environmental conditions in that population. In our study, surprisingly, the percentage of germination in the SCV stand during 2008 was higher than expected, being the highest found in the literature for *N. antarctica*. This great variation between years in the same stand suggests a decisive influence (direct or indirect) of some environmental driver. But unfortunately it was not detected in the present work. There are antecedents indicating a close direct relationship between the seeds size and its further germination or viability (Cellini 2010), as well as interactions among seeds size and environmental conditions (i.e., light) (Pearson et al. 2002).

As has been previously reported (Bahamonde et al. 2011) the proportion of fallen seeds at each month was independent of the production every year. Donoso et al. (2006) have suggested that the period of seed fallen in *N. antarctica* would vary as a function of the latitude and biotope where the stands are located.

Changes in seed production and quality due to thinning

In general, the differences in forest structure between PF and SP was not reflected in seed production in both site quality classes. Thus, it would be valid to say that individually the trees growing in the silvopastoral stands produced higher quantity of seeds compared to the trees in PF. These results were different to the published by Soler et al. (2013) for *N. antarctica* forests in Tierra del Fuego, who informed that PF produced more seeds compared to silvopastoral use stands in a period of 3 years. According these authors such differences may be related to the major basal area (and in consequence major crown cover) in the PF compared to the silvopastoral one. In our study, the lower basal area and crown cover in SP stands (Bahamonde et al. 2015) did not imply less seed production. There is information assigning an important role in the seed production to the size of the individual plants (Weiner 1988). Moreover, in the case of trees seed production some authors uses only measurements in dominants and co dominant trees (Greene and Johnson 1994). In our work, the proportion of dominant and co-dominant trees were higher in the SP stands (especially in SCV), which could explain in part the obtained results. In the same way, litterfall production evaluated in the same stands and years showed a similar pattern (Bahamonde et al. 2015).

In general, the change of the structure derived from the different stand uses did not modify the size of seeds, keeping it within the range found in the literature. In the case of seeds germination, different patterns were found among site classes. In SCIV, the trend was not different among uses, but in SCV there were differences among years and uses. There are not antecedents about seeds germination in *N. antarctica* during several years. Soler et al. (2013) did not find differences in the parameter "non-viable seeds" between different uses of ñire forests in Tierra del Fuego in a period of 3 years, although significant differences between years were informed. In a noticeable long period study (45 years) in *N. solandri* forests, Allen et al. (2014) reported a great inter annual variation in the production of viable seeds. Also these authors published that the changes in viable seeds were associated to rainfall and temperatures.

Regeneration in PF

There was very low (or null) generalized establishment of seedlings and their survival during the following years in the evaluated stands independently of the site quality class where forests were growing. This contrast with Soler et al. (2013) in Tierra del Fuego, where they measured seedlings establishment during 3 years in a primary *N. antarctica* forest in a site equivalent to our SCIII, with an average value of 2.6 million ha^{-1}. The scarce existing antecedents about seedlings establishment in *N. antarctica* forests highlighted the low reproductive success through seeds, being its main reproductive strategy the vegetative regrowth (Veblen et al. 1996; Donoso et al. 2006).This is consistent with the latest inventory in *N. antarctica* forests in Santa Cruz province, where Peri and Ormaechea (2013) informed that 40 % of the total surface of ñire forest has scarce or null regeneration, and 70 % of the total regeneration when exists is related to fire. Also there are antecedents evidencing favorable resprouting of stumps after thinning practices in Santa Cruz (Bahamonde et al. 2013b). Beside this, it is possible that in better growing conditions (i.e., higher rainfall through the year) as in Tierra del Fuego, the natural regeneration can be the main reproduction strategy for these forests (Soler et al. 2013).

Changes in regeneration due to thinning

Although it was not possible to analyze statistically the establishment and survival of seedlings between PF and silvopastoral stand, it was evident that the canopy openness of silvopastoral stands favored the establishment of seedlings in both site classes. This pattern had already been previously reported in a shorter study in these sites (Bahamonde et al. 2013a). Similarly, Soler et al. (2013) informed higher establishment success in silvopastoral stands compared to PF of *N. antarctica* in Tierra del Fuego. Also these authors reported very low percentage of seedlings survival during the two subsequent years, with not differences among PF and SP stands. This is concordant with the literature indicating that in general the *Nothofagus* spp. have more successful establishment of seedlings in high light and soil moisture conditions (Veblen et al. 1996; Cuevas 2000; Martínez Pastur et al. 2011), although in our study the soil moisture did not differ between PF and SP stands. Particularly *N. antarctica* has been labeled as an specie with low tolerance to the shade (Frangi et al. 2004). The generalized very low survival of seedlings was not related to the soil moisture because its values were in a range considered adequate for growth. However, we can speculate that may be caused by the high competition with the understory grasses proliferating specially in more open areas. Particularly, in the studied sites there are antecedents reporting that the aerial biomass of grasses inside the forest was similar to the measured in open areas surrounding the forest (Bahamonde et al. 2012).

Correlations between structural, environmental and seeds

The global analysis allow us to determine the positive association between seedling establishment and the seed production and its quality (size and germination), and explain the scarce reproductive success in the studied sites, which may be due to a general low seed production, seed weight and germination rate. About this, there are antecedents indicating that bigger seeds have more success in establishment and survival of seedlings for different species (Osunkoya et al. 1994; Walters and Reich 2000). Similarly, Pearson et al. (2002) reported an interaction between different light levels and seeds size on the germination of 16 species of pioneer trees in semi-deciduous rain forest in Panama. On the other hand, the negative correlation between the quality of seeds (size and germination) and total volume of wood (combination of density and tree size) was because the PF in SCIII and SCIV (greater volume stands) produced lighter seeds with low germination. Although we included the litterfall production in this analysis to check if it was related to the seed production but no correlation was found. The significant correlations between litterfall production and structural variables have been discussed in Bahamonde et al. (2015). The positive correlation between crown cover and soil moisture could be due to the decrease of strong winds by the trees in these stands (Bahamonde et al. 2009) which reduce water loss from evaporation. The negative correlation between litterfall production and the soil moisture at the beginning of seedling establishment could reflect higher level of rainfall interception at the soil level.

The 10 years of measurements and antecedents suggest that in Santa Cruz province the regeneration of *N. antarctica* forests from seeds is strongly restricted by several factors. On the one hand, seed production and its quality would restrict the seedling installation. Soler et al. (2013) reported several factors affecting seedling establishment such as flowers production, losses by predation (i.e., insects, birds, mice) and losses due to environmental conditions (i.e. stratification during winter). On the another hand, the thinning practices that open the canopy for silvopastoral use improved the conditions (specially availability of light) for the establishment of seedlings, but at the same time the canopy openness stimulates the understory growing, which would restrict the seedlings survival. In Tierra del Fuego Soler et al. (2013) informed major success of seedling establishment and survival in silvopastoral stands compared to primary and secondary forests.

In any case, the silvopastoral use of these forests implies the introduction of cattle, which have negative consequences for regeneration. Echevarria et al. (2012) determined that high animal stocking rate (>0.6 bovine units ha^{-1} year^{-1}) affected negatively the surviving and growth of *N. antarctica* regeneration in silvopastoral systems in Chubut province. In this context, management practices are necessary to guarantee the continuity of the arboreal stratum. There are antecedents where individual protections in regeneration have been used (Martínez Pastur et al. 2013). These authors reported that protected saplings had higher mean annual growth in height (10.1 cm) compared to unprotected saplings (0.4 cm), mainly after the second year of protections setting up.

Conclusions

In general terms the site quality of the studied forests did not influence their seed production and regeneration. The amount of seed production and seed quality were proved to have a decisive influence on the *N. antarctica* seedling establishment in the subsequent year. At the same time, our results suggest that independently of the site class where the stands are growing, the canopy openness for silvopastoral use improve the conditions for seedling establishment. However, the success of seedling survival over time would be conditioned for the influence of another factors not measured here (e.g., understory competition, drought). Finally, the results suggest that management of regeneration is necessary to ensure continuity of arboreal stratum in *N. antarctica* forests under silvopastoral use. Further studies are still needed to better understand the reproductive strategies of this species.

References

Acosta MC, Mathiasen P, Premoli AC (2012) Predominant regeneration strategy results in species-specific genetic patterns in sympatric *Nothofagus* ss congeners (*Nothofagaceae*). Aust J Bot 60(4):319–327

Allen RB, Hurst JM, Portier J, Richardson SJ (2014) Elevation-dependent response of tree mast seeding to climate change over 45 years. Ecol Evol 4:3525–3537

Bahamonde HA, Peri PL (2013) Receptividad ganadera en bosques de *Nothofagus antarctica* (ñire) bajo uso silvopastoril en Patagonia Sur basado en los requerimientos energéticos de los animales. Proceedings Cuarto Congreso Forestal argentino y latinoamericano, Iguazú, Misiones. 10 pp. ISSN 1669 6786. Web documents. http://www.researchgate.net/publication/257307374_RECEPTIVIDAD_GANADERA_EN_BOSQUES_DE_Nothofagus_antarctica_%28ire%29_BAJO_USO_SILVOPASTORIL_EN_PATAGONIA_SUR_BASADO_EN_LOS_REQUERIMIENTOS_ENERGTICOS_DE_LOS_ANIMALES. Accessed 17 Oct 2014

Bahamonde HA, Peri PL, Martínez Pastur G, Lencinas V (2009) Variaciones microclimáticas en bosques primarios y bajo uso silvopastoril de *Nothofagus antarctica* en dos Clases de Sitio en Patagonia Sur. Documentos INTA web.http://inta.gob.ar/documentos/variaciones-microclimaticas-en-bosques-primarios-y-bajo-uso-silvopastoril-de-nothofagus-antarctica-en-dos-clases-de-sitio-en-patagonia-sur/. Accessed 10 Oct 2013

Bahamonde HA, Peri PL, Monelos LH, Martínez Pastur G (2011) Aspectos ecológicos de la regeneración por semillas en bosques nativos de *Nothofagus antarctica* en Patagonia Sur, Argentina. Bosque 32:20–29

Bahamonde HA, Peri PL, Alvarez R, Barneix A (2012) Producción y calidad de gramíneas en un gradiente de calidades de sitio y coberturas en bosques de *Nothofagus antarctica* (G. Forster) Oerst. en Patagonia. Ecol Austral 22:62–73

Bahamonde HA, Peri PL, Monelos LH, Martínez Pastur G (2013a) Regeneración por semillas en bosques nativos de *Nothofagus antarctica* bajo uso silvopastoril en Patagonia Sur, Argentina. Bosque 34:89–101

Bahamonde HA, Peri PL, Monelos L, Gargaglione V (2013b) Crecimiento en rebrotes vegetativos de *Nothofagus antarctica* (ñire, ñirre) desde el tocón después de un raleo. In: Peri PL (ed) 2nd Congress on Patagonian Agroforestry (International), El Calafate, INTA Editions, p 93

Bahamonde HA, Peri PL, Martínez Pastur G, Monelos LH (2015) Litterfall and nutrients return in *Nothofagus antarctica* forests growing in a site quality gradient with different management uses in Southern Patagonia. Eur J Fort Res 134(1):113–124

Cellini JM (2010) Estructura y regeneración bajo distintas propuestas de manejo de bosques de *Nothofagus pumilio* (Poepp. et Endl.) Krasser en Tierra del Fuego, Argentina. Doctoral thesis. Facultad de Ciencias Naturales y Museo, Universidad de La Plata, Buenos Aires. p 157

Collado L (2001) Los Bosques de Tierra del Fuego. Análisis de su estratificación mediante imágenes satelitales para el inventario forestal de la Provincia. Multequina 10:1–16

Cuevas JG (2000) Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego Chile. J Ecol 88(5):840–855

Donoso C, Escobar B (2006) *Nothofagus nitida* (Phil) Krasser. Coigüe de Chiloé. In: Donoso Zegers C (ed). Las especies arbóreas de los bosques templados de Chile y Argentina.Autoecología. Valdivia pp 462–470

Donoso C, Steinke L, Premoli A (2006) *Nothofagus antarctica* (G. Forster) Oerst. In: Donoso Zegers C ed. Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología. Valdivia, pp 401–410

Echevarria D, von Müller A, Hansen N, Bava J, Escalona M (2012) Efectos delherbívoro sobre la regeneración de ñire bajo diferentes situaciones de manejo. Proceedings of the 2nd national congress of silvopastoral systems, Santiago del Estero, INTA Editions, pp 311–316

Frangi JL, Barrera MD, Puigdefábregas J, Yapura PF, Arambarri AM, Richter LL (2004) Ecología de los bosques de Tierra del Fuego. In: Arturo M, Frangi J, Goya JF (eds) Ecología y Manejo de los Bosques de Argentina. Web documents. http://sedici.unlp.edu.ar/bitstream/handle/10915/15915/Ecolog%C3%ADa_de_los_bosques_de_Tierra_del_Fuego__Jorge_L._Frangi__Marcelo_D._Barrera__Juan_Puigdef%C3%A1bregas__Pablo_F._Yapura__Ang%C3%A9lica_M._Arrambari_y_Laura_Richter_.pdf?sequence=20. Accessed 17 Sept 2013

Greene DF, Johnson EA (1994) Estimating the mean annual seed production of trees. Ecology 75(3):642–647

Gurevitch J, Chester ST Jr (1986) Analysis of repeated measures experiments. Ecology 67:251–255

Henríquez CA (2004) Efecto de la fragmentación del hábitat sobre la calidad de las semillas en *Lapageria rosea*. Rev chil Hist Nat 77:177–184

Herrera CM, Jordano P, Guitián J, Traveset A (1998) Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. Am Nat 152(4):576–594

Ivancich H, Martínez Pastur G, Peri PL (2011) Modelos forzados y no forzados para el cálculo de índice de sitio en bosques de *Nothofagus antarctica* en Patagonia Sur. Bosque 32:135–145

Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? Annu Rev Ecol Evol Syst 33:427–447

Leishman MR, Wright IJ, Moles AT, Westoby M (2000) The evolutionary ecology of seed size. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, pp 31–57

Lencinas VM, Martinez Pastur G, Cellini JM, Vukasovic R, Peri PL, Fernandez MC (2002) Incorporación de la altura dominante y la clase de sitio a ecuaciones estándar de volumen para *Nothofagus antarctica*. Bosque 23:5–17

Marchelli P, Gallo LA (1999) Annual and geographic variation in seed traits of Argentinean Populations of southern beech *Nothofagus nervosa* (Phil.) Dim. etMil. For Ecol Manag 121(3):239–250

Martínez Pastur G, Peri P, Cellini JM, Lencinas MV, Barrera M, Ivancich H (2011) Canopy structure analysis for estimating forest regeneration dynamics and growth in *Nothofagus pumilio* forests. Ann For Sci 68:587–594

Martínez Pastur G, Peri P, Lencinas MV, Cellini JM, Barrera M, Soler Esteban R, Ivancich H, Mestre L, Moretto AS, Anderson CB, Pulido F (2013) La producción forestal y la conservación de la biodiversidad en los bosques de *Nothofagus* en Tierra del Fuego y Patagonia Sur. In: Donoso P, Promis A (eds) Silvicultura en bosques nativos: Avances en la investigación en Chile, Argentina y Nueva Zelanda. Universidad Austral de Chile, Valdivia, 8, pp 155–179. ISBN 978-956-7173-32-7

Masaki T, Oka T, Osumi K, Suzuki W (2008) Geographical variation in climatic cues for mast seeding of *Fagus crenata*. Popul Ecol 50:357–366

Osunkoya OO, Ash JE, Hopkins MS, Graham AW (1994) Influence of seed size and seedling ecological attributes on shade-tolerance of rainforest tree species in Northern Queensland. J Ecol 82:149–163

Pastorino M, Gallo L (2000) Variación geográfica en peso de semilla en poblaciones naturales argentinas de "Ciprés de la Cordillera". Bosque 21(2):95–109

Pearson TRH, Burslem DFRP, Mullins CE, Dalling JW (2002) Germination ecology of neotropical pioneers: interacting effects of environmental conditions and seed size. Ecology 83(10):2798–2807

Peri PL, Ormaechea SG (2013) Relevamiento de los bosques nativos de ñire (*Nothofagus antarctica*) en Santa Cruz: base para su conservación y manejo. Ediciones INTA web. http://inta.gob.ar/documentos/libro-201crelevamiento-de-los-bosques-nativos-de-nire-nothofagus-antarctica-en-santa-cruz-base-para-su-conservacion-y-manejo201d. Accessed 17 Nov 2014

Peri PL, Hansen N, Rusch V, Tejera L, Monelos L, Fertig M, Bahamonde HA, Sarasola M (2009) Pautas de manejo de sistemas silvopastoriles en bosques nativos de *Nothofagus antarctica* (ñire) en Patagonia. Documentos INTA web. http://inta.gob.ar/documentos/pautas-de-manejo-de-sistemas-silvopastoriles-en-bosques-nativos-de-nothofagus-antarctica-nire-en-patagonia/. Accessed 17 Oct 2013

Peri PL, Lencinas MV, Martínez Pastur G, Lasagno R, Soler R, Bahamonde HA (2014) Red PEBANPA: Parcelas de Ecología y Biodiversidad de ambientes naturales en Patagonia Austral. Proceedings XXVI Reunión argentina de Ecología RAE 2014, Comodoro Rivadavia, Argentina, 3 a 5 de Noviembre de 2014. ISBN 978-987-1937-40-0. p 220

Peri PL, Bahamonde HA (2012) Digestibilidad de gramíneas creciendo en bosques de ñire (*Nothofagus antarctica*) bajo uso silvopastoril. In: Proceedings of the 2nd national congress of Silvopastoral systems, Santiago del Estero. INTA Editions, pp 264–269

Premoli A (1991) Morfología y capacidad germinativa en poblaciones de *Nothofagus antarctica* (Forster) Oerst del noroeste andino patagónico. Bosque 12(2):53–59

Premoli AC, Steinke L (2008) Genetics of sprouting: effects of long-term persistence in fire-prone ecosystems. Mol Ecol 17(17):3827–3835

Raffaele E, Veblen TT (2001) Effects of cattle grazing on early post fire regeneration of matorral in northwest Patagonia, Argentina. Nat Areas J 21:243–249

Ramírez C, Correa M, Figueroa H, San Martín J (1985) Variación del hábito y hábitat de *Nothofagus antarctica* en el centro del Sur de Chile. Bosque 6(2):55–73

Richardson SJ, Allen RB, Whitehead D, Carswell FE, Ruscoe WA, Platt KH (2005) Climate and net carbon availability both determine seed production in a temperate tree species. Ecology 86:972–981

Soler R, Martínez Pastur G, Peri PL, Lencinas MV, Pulido F (2013) Are silvopastoral systems compatible with forest regeneration? An integrative approach in southern Patagonia. Agrofor Syst 87:1213–1227

Steinke L (2004) Morphological and isozyme variation of *Nothofagus antarctica* in different habitats in Northern Patagonia Examensabete Ekosystemteknik Ekologi. Lund University, Lund

Steinke LR, Premoli AC, Souto CP, Hedrén M (2008) Adaptive and neutral variation of the resprouter *Nothofagus antarctica* growing in distinct habitats in north-western Patagonia. Silva Fenn 42(2):177–188

Veblen TT, Donoso C, Kitzberger T, Rebertus AJ (1996) Ecology of Southern Chilean and Argentinean *Nothofagus* forests. In: Veblen TT, Hill RS, Read J (eds) The ecology and biogeography of *Nothofagus* forests. Yale University, New Haven, pp 293–353

Walters MB, Reich PB (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. Ecology 81(7):1887–1901

Weiner J (1988) The influence of competition on plant reproduction. In: Lovett Doust JL, Lovett Doust L (eds) Plant reproductive ecology. Oxford University, Oxford, pp 228–245

Willems P, Raffaele E (2001) Implicancias del efecto de las interacciones en la interpretación de experimentos factoriales en biología. Ecol Austral 11:131–138